FURTHER CONTRIBUTIONS TO THE MORPHOLOGY OF THE DEGENERIACEAE

B. G. L. SWAMY

With four plates and thirteen text-figures

DURING HIS COLLECTING TRIP in the Fiji Islands in 1947,[1] Dr. A. C. Smith was able to pickle valuable material of *Degeneria vitiensis* I. W. Bailey & A. C. Sm. This material includes not only leaves, nodes, shoot apices, seedlings, etc., but also flowers and fruits in almost all stages of development. Although most of the material was fixed in formalin-acetic-alcohol, limitation of resources in one case forced Dr. Smith to substitute "gin" when he secured important developmental stages of the gametophytes. However, the gin-fixed material has fortunately rendered itself suitable for interpretation, although the slides may not satisfy all the requirements of technical perfection. The material on hand has made possible not only a verification of the original findings of Bailey and Smith (1), but also new observations on the gametophytic and post-fertilization development, vascularization of the flower, seedling structure, etc. I sincerely thank Dr. Smith for placing the material at my disposal and thereby providing me with the opportunity of studying it. I cannot adequately express my gratitude and appreciation to Prof. I. W. Bailey for his unfailing encouragement and illuminating suggestions during this study and also for his assistance in the preparation of photomicrographs.

SECONDARY XYLEM

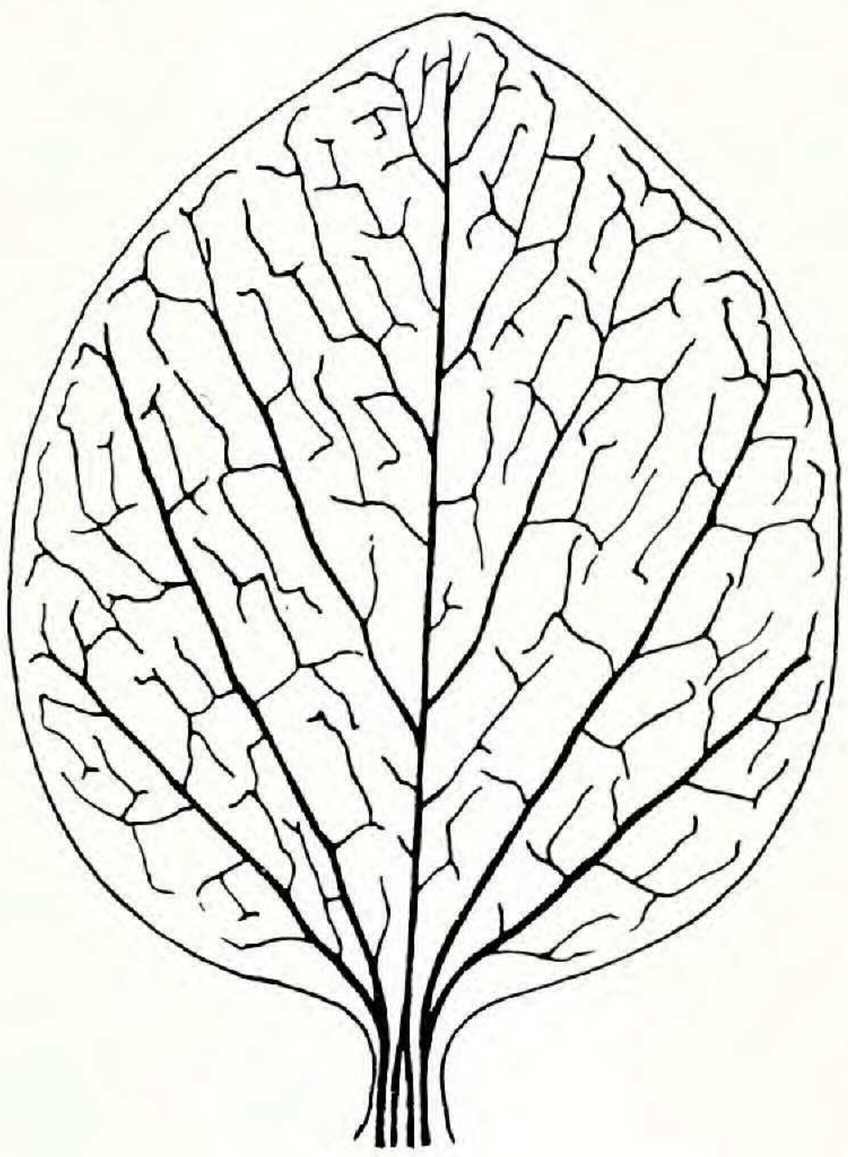
There is not much to be added to the anatomical characteristics of the secondary xylem, which have already been described by Bailey and Smith (1). However, the following points as revealed by the peripheral regions of a large stem measuring about 60 cm. in diameter (#5880),[2] may be noted. In the inner regions of the secondary xylem, the multiseriate rays are predominantly 3–4-seriate, fairly high, usually with one to three upright cells at either end as seen in tangential sections; the uniseriate rays are infrequent, shorter than the multiseriates and composed of upright cells. In the outermost region of this old specimen, the multiseriate rays become predominantly 4–5-seriate, shorter and without any upright cells at the margins. Uniseriate rays are eliminated. The narrow bands of apotracheal parenchyma are distributed throughout the secondary xylem. This situation is in contrast to the secondary xylem of the magnoliaceous genera of the north temperate climate, where the parenchyma is confined to the outer face of the growth rings.

[1] See the preceding article in this journal.

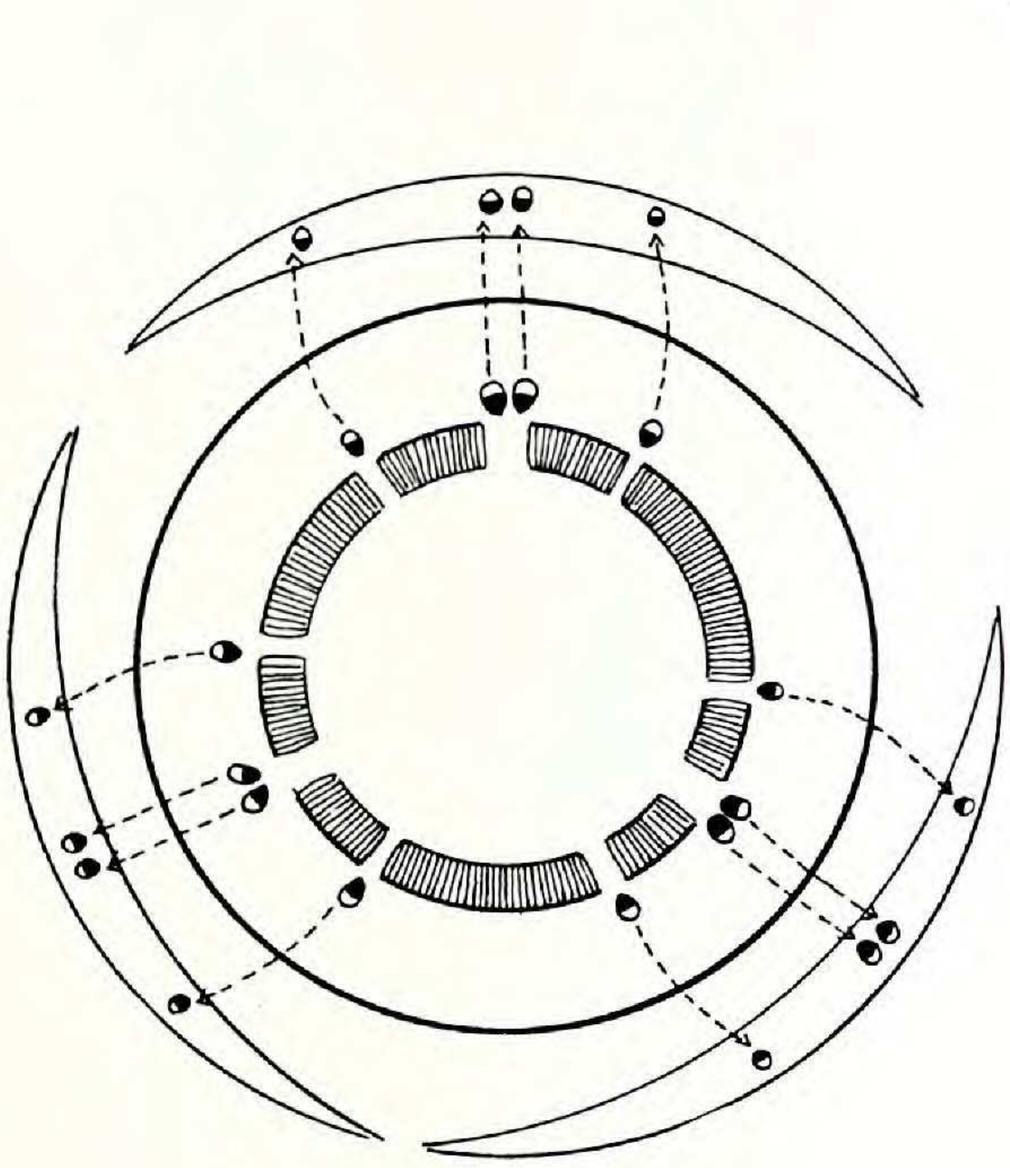
[2] In the few instances where it has seemed advisable to refer to a specific collection, the number indicates Dr. Smith's field-number. For locality, etc., see the preceding paper in this journal.

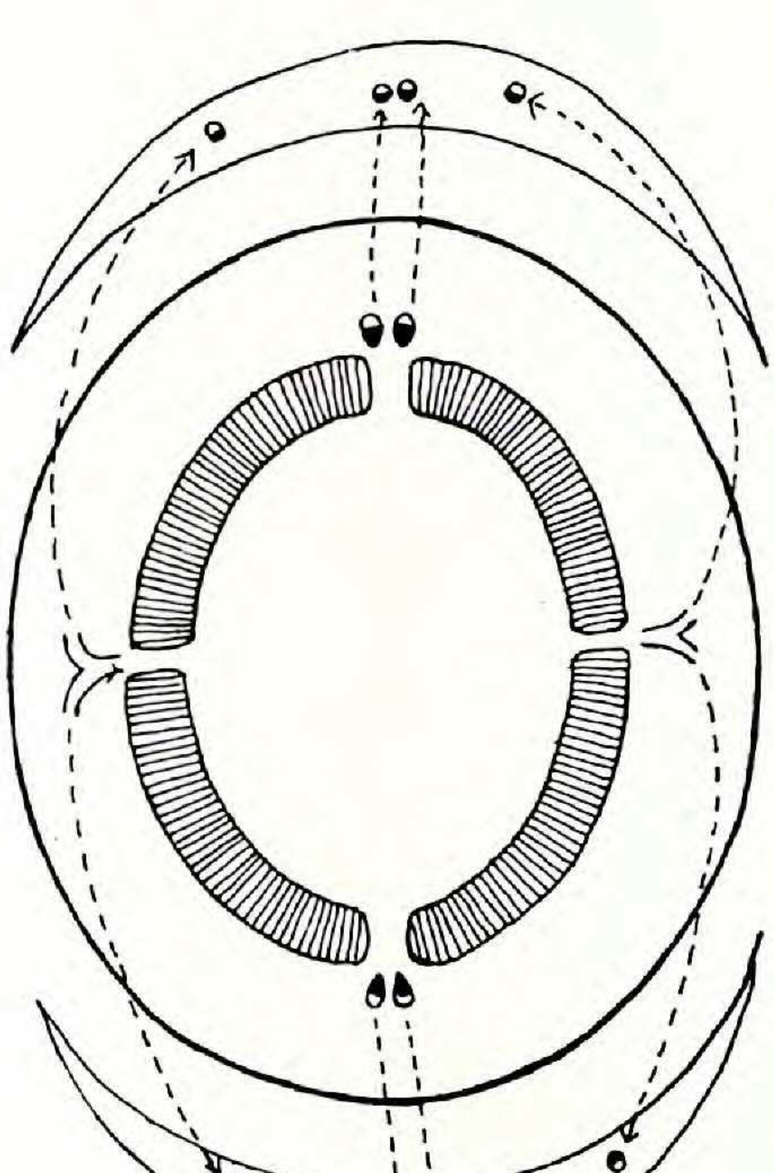
SEEDLING

Four seedlings of *Degeneria* were available for examination and all of them possess three cotyledons. The whorl of thin, palmately veined cotyledons is preceded by a long hypocotyl, 6–10 cm. The first leaf is characteristically emarginate, pinnately veined, and more nearly elliptic in



1a





1 2

FIGS. 1–2. *Fig. 1.* Diagram showing the vascular pattern of the cotyledonary node of *Degeneria*. *Fig. 1a.* Diagram to show the pattern of vascularization in the cotyledon, × 5. *Fig. 2.* Diagram showing the vascular pattern of the cotyledonary node in *Magnolia grandiflora*.

outline. The subsequent leaves soon assume the elliptic to obovate-elliptic norm of the genus.

Two median vascular traces originating from a single gap in the stele enter each cotyledon. These strands remain distinct in the petiole, *Figs.* 1, 1a, but unite in the basal part of the lamina into a single strand which then forms the median vein of the cotyledon. The phloem of the strand maintains its doubleness till about half the distance in the cotyledon and then unites. The marginal traces of the cotyledons arise from separate gaps in the stele, *Fig.* 1, and bifurcate in the basal part of the lamina, *Fig.* 1a; the bifurcated strands diverge in the blade in a palmate fashion. The branches of these lateral strands vascularize most of the lower half of the blade. The remainder of the cotyledon is vascularized by the branch system of the median strand, *Fig.* 1a.

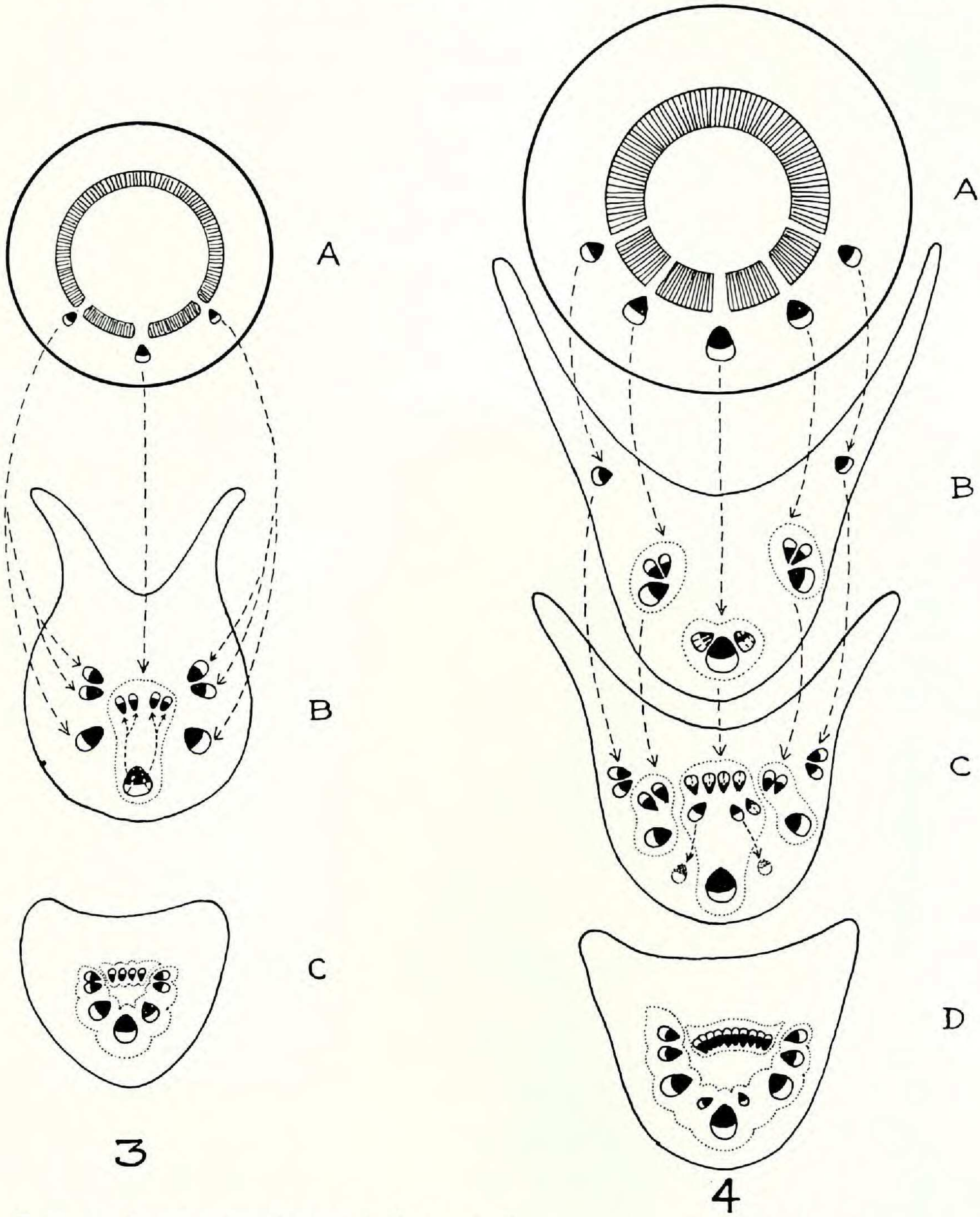
The seedlings of the Magnoliaceae (*Magnolia, Michelia, Liriodendron*) are provided with two cotyledons in the great majority of cases, *Fig.* 2. The median pair of strands originates in the same manner as in *Degeneria,* but the four lateral strands of the two cotyledons are derived by the bifurcation of two traces which arise from two gaps in the stele. Even in those abnormal instances of tricotyledonous seedlings which are now and then encountered in *Magnolia stellata,* the lateral traces of the adjacently placed cotyledons arise in the same way. This pattern seems to be stabilized fairly well in the family, although *Magnolia Soulangeana* (7) appears to possess a nodal anatomy similar to *Degeneria.*

ANATOMY OF THE NODE AND PETIOLE

The first few leaves of the seedling receive three traces from a corresponding number of gaps in the stele, *Fig.* 3A, and thus the nodes on which these leaves are borne are trilacunar. In serially arranged transverse sections of the petiole, the three traces exhibit the following changes in their courses outward into the leaf. The median trace trifurcates, forming a large central strand and two smaller lateral ones. The lateral strands, from a purely descriptive point of view, appear to shift adaxially toward the upper part of the petiole and split into four small bundles having an inverted orientation of xylem and phloem, *Fig.* 3B. The lateral traces (compare *Figs.* 3A and 3B) bifurcate, and the more adaxially situated products of this division subsequently divide, forming a total of six strands, three on each side of the derivatives of the median trace. Higher in the petiole, the large abaxial segment of the median trace and the branches of the lateral traces converge in the form of a large arc of seven strands, *Fig.* 3C. This arc is closed by the four smaller derivative strands of the median trace, thus giving rise to an adaxially flattened eustele.

In contrast to the seedling nodes, those on the mature stem are pentalacunar, *Fig.* 4A, as reported by Bailey and Smith (1), although very large leaves of vigorously growing saplings may receive more than five bundles from the corresponding nodes. With increase in the number of traces the vascularization pattern of the petiole becomes more complex. The median trace trifurcates at the base of the petiole, *Fig.* 4B, the lateral

segments of which break up into a varying number of eight to twelve strands. These smaller strands aggregate in the upper part of the petiole, the individual strands orienting to form a loose "inner eustele," *Fig.* 4C. The second pair of laterals also divide. At a higher level, two to four strands from the "inner eustele" swing back into an abaxial position on either side of the median trace, as indicated by broken arrows in *Fig.* 4C. The paired adaxial segments of the first pair of laterals join the corre-

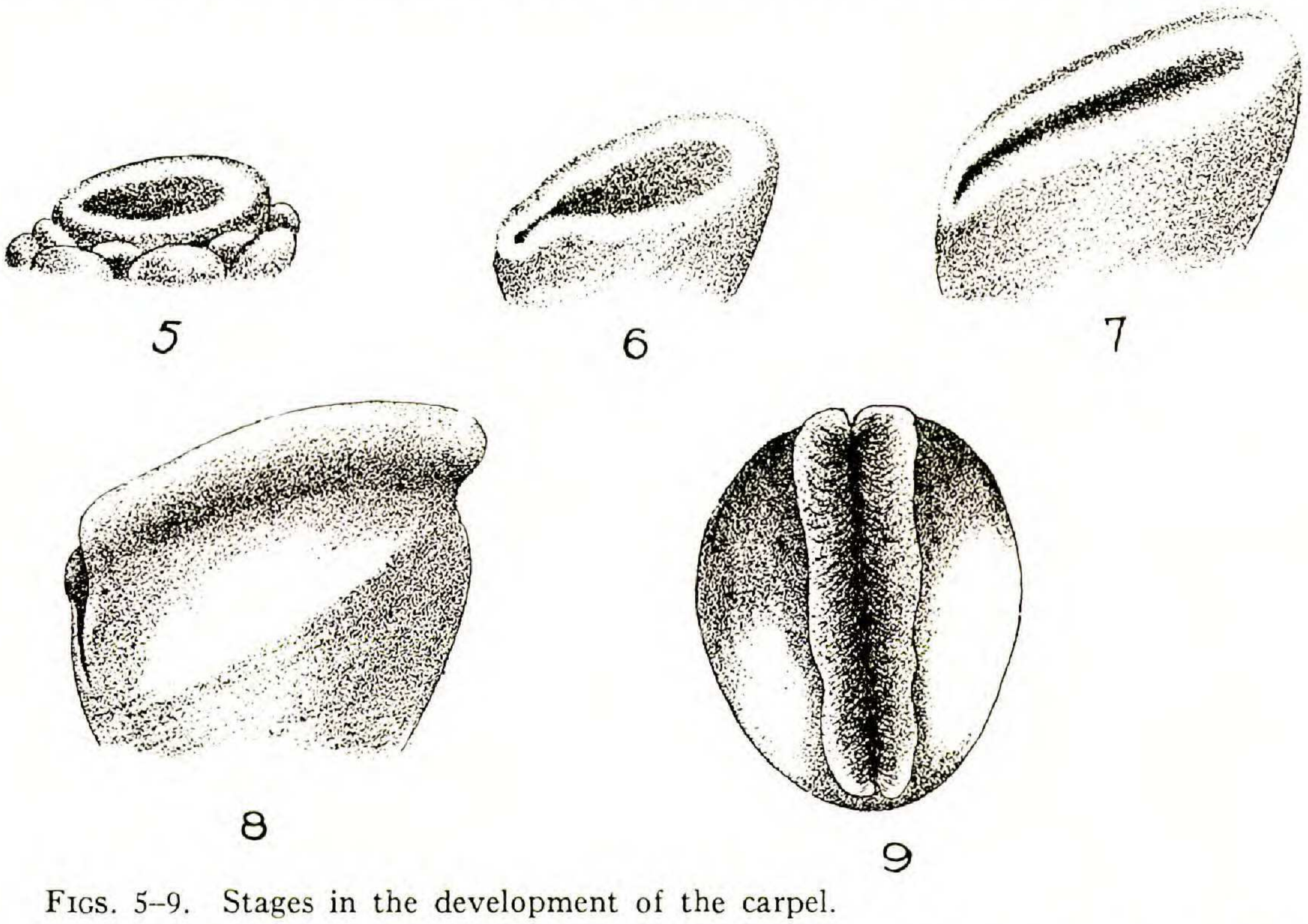


FIGS. 3, 4. *Fig. 3.* Series of diagrams illustrating the behavior of the vascular traces at the node and in the petiole of a seedling leaf. A represents the nodal level; B and C, basal and upper levels of the petiole. *Fig. 4.* Same; in the adult leaf. A represents the nodal level; B, C, and D, successively higher levels in the petiole.

sponding ends of the now more or less opened "inner eustele" in the form of a strap, which occupies the flattened upper side of the petiole. The remainder of the traces unite into a large horse-shoe-shaped arc, the ends of which approximate the lateral extremities of the strap-shaped segment, thus forming an adaxially flattened eustele, *Fig*. 4D. In spite of these complications, the fundamental pattern — trifurcation of the median trace and the organization of the adaxial strap-shaped segment largely by the lateral segments of the median trace — is the same in both the seedling and the adult leaves. In the latter, the number of bundles involved is decidedly larger and a few of the strands of the median system swing back into an abaxial position, which situation has no counterpart in the trilacunar seedling leaves.

ORGANOGENY

The first structures to develop on the thalamus are the calyx members. The differentiation of the petals takes place in quick succession, the outermost members originating first, *Fig*. 82. There seems to be a time lag before the initiation of the androecium, during which period the corolla completely envelops the broad, mound-shaped floral apex, *Fig*. 83. The ontogenetic differentiation of the staminal whorls is also in a centripetal



FIGS. 5–9. Stages in the development of the carpel.

succession. Some of the last-formed members of the androecium later transform themselves into staminodes. After the initiation of the androecium, *Fig*. 84, the floral apex is rendered narrower and somewhat blunt. This apex is used up in the organization of the solitary carpel, *Fig*. 85. Thus the order of development of calyx, corolla, androecium and gynoecium, as well as of the individual whorls of corolla and androecium, is in centripetal succession.

As a result of the confinement of meristematic activity to the rim of the carpel primordium, an embossed periphery is created. At this stage, the primordium appears as a shallow cup, having an outline similar to that of a horse-shoe, the free ends of which are fused, *Fig*. 5. A few cells on this ventral side fail to divide but the surrounding cells continue divisions; as a result, a notch appears in the wall of the cup, *Fig*. 6. Furthermore, the cells of the rim on the dorsal side maintain a faster rate of division and the tissue on this side grows rapidly in height. This results in a conduplicate structure enclosing a cavity between the folds. The structure itself is abaxially deformed, *Fig*. 7. The free edges grow out externally in the form of flanges, whose margins flare apart, *Figs*. 8, 9. A transverse section of the carpel at this stage is represented in *Fig*. 89. The internal surfaces of the flanges later become stigmatic, as will be described on a subsequent page.

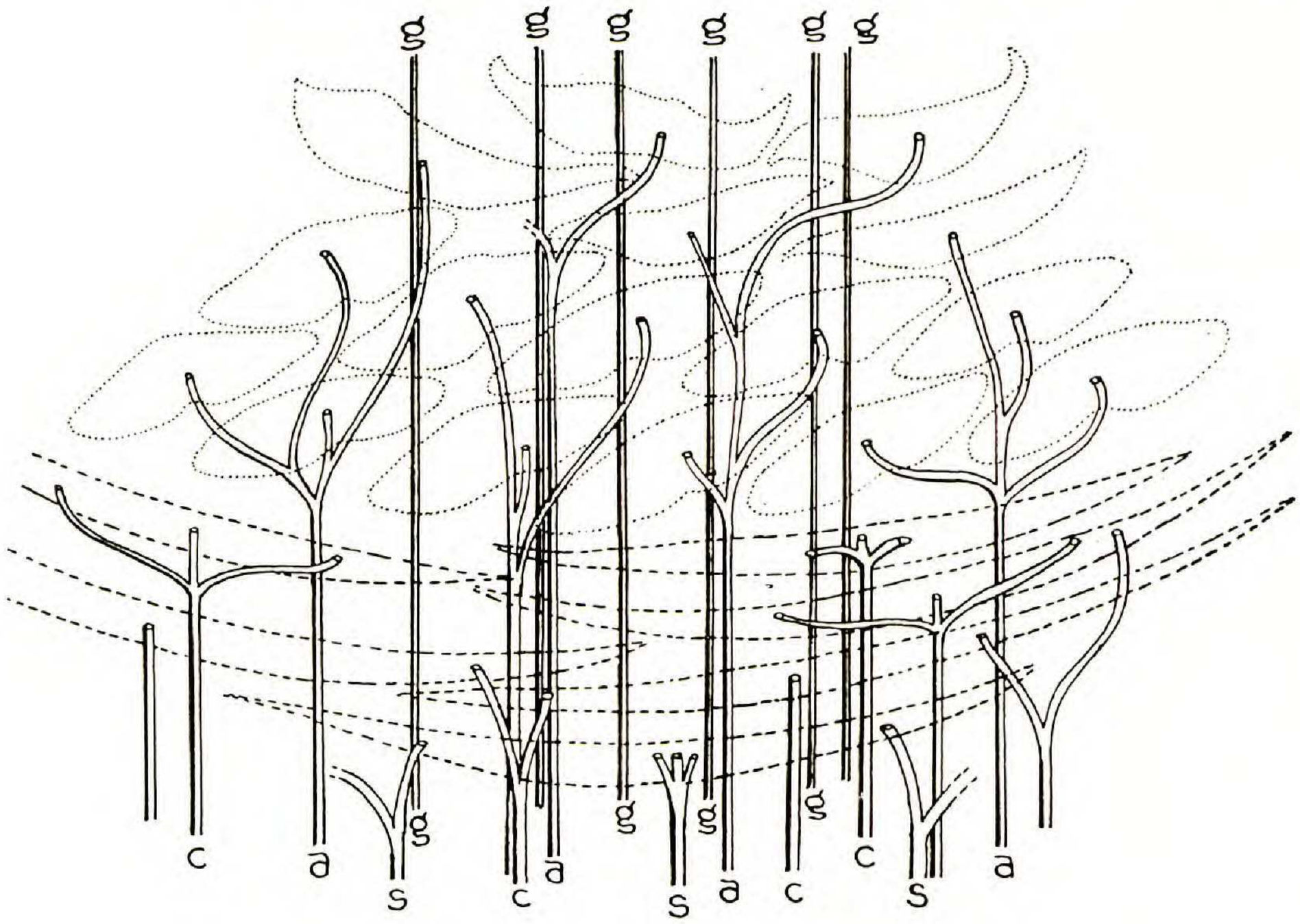
VASCULARIZATION OF THE FLOWER

An ontogenetic outlook in studies dealing with the vascular anatomy of flowers is an essential factor for an understanding of the real significance of the phenomena involved. The procambial system laid down during the early development is subject to a high degree of modification as the flower attains maturity. The modifications involve either an elaboration of the system which brings greater complexities into the adult vascular structure, or a reduction whereby the mature vasculature becomes very much simplified. In order to emphasize the degree and nature of the complications that attend the procambial pattern of the *Degeneria* flower, the topic will be considered at present under two heads — the procambial pattern and the vascular pattern at anthesis. The adaptation of this method should not be interpreted as implying that all the organs of the flower have their vasculature represented only by the procambial strands at any one single step and that the strands become differentiated into xylem and phloem at another single step. In fact, hand in hand with the extension of the procambial strands into the newly formed structures on the floral axis, the older portions of the same strands become transformed into xylem and phloem. This being the case, it would be misleading to look at the phenomenon as involving two definite steps. The distinction made at present is only for the sake of description.

Procambial pattern:

Figure 10 represents what may be called the "procambial diagram" of a sector of the flower. This diagram is synthesized after following the course of differentiation and extension of the procambium into the respective structures of the flower as they are being formed on the thalamus; the secondary modifications of these strands have been deliberately omitted in this figure, but have been incorporated in the diagram representing the vascular pattern at anthesis, *Fig*. 11.

In general, the method of supply of the procambial strands to the sepals and petals is very similar. Each member receives a median and two mar-



FIGS. 10, 11. *Fig. 10.* Procambial diagram of a sector of a flower, depicted as seen from the side with one of the calyx lobes facing the reader. *s* — vascular traces supplying the sepal members; *c* — of petal members; *a* — of androecial members; *g* — of gynoecium. *Fig. 11.* Vascular diagram of the same sector at anthesis. Lettering as in Fig. 10.

ginal traces, *Fig.* 10 (traces of the sepals marked *s*, of the corolla, *c*). The marginal traces of the adjacently placed members are usually derived from a common stelar bundle. However, each of the petals belonging to the innermost whorl receives a single bundle, which trifurcates into median and marginal traces. Each member of the androecium receives a single trace. It may be noted that the supply of a group of four or five stamens originates from a single stelar bundle (marked *a*). The remainder of the procambial bundles (marked *g*) fuse with each other into seven to nine larger units before entering the carpel.

Vascular pattern at anthesis:

By the time the flower bud attains the stage of anthesis, the simple pattern of vascularization just described becomes highly modified, of course, retaining the original ground plan in all essentials (compare *Figs.* 10 and 11; the latter diagram represents the same sector of the flower as that depicted in the former). The important modifications that are involved may be briefly stated as follows.

PERIANTH. — The vasculature of the perianth members is subject to a high degree of modification. The median and marginal traces of each member branch, and the branches anastomose not only with one another but also with similar branches belonging to the members of the adjacent whorls. Numerous new traces originate from the points of anastomoses and occupy positions on either side of the median and marginal traces of each perianth lobe.

ANDROECIUM. — In the androecial members, the modification is less pronounced. The single vein trifurcates into the median and marginal traces at the very base of the microsporophyll. In the staminodes, the marginal traces undergo a further bifurcation at the base and are generally more highly developed than in the stamens.

In this connection some points in the ontogeny of the stamens and staminodes may be considered. The primordia of all the individual members of the androecium are alike in shape, size and histological characteristics. The cells are richly protoplasmic and show a great and uniform avidity for stains. With subsequent development, parenchymatization starts in the adaxially situated cells and proceeds in an abaxial direction. When this phenomenon advances to about half the distance between the abaxial and adaxial surfaces, a nest of small cells in the center becomes differentiated as the procambial strand. It is at about this time that the archesporial cells begin to differentiate in the hypodermal layer on the abaxial side. The archesporial cells undergo the first periclinal division, leading to the formation of the primary parietal and sporogenous layers. The development until this stage is characteristically seen to take place in all the primordia of the androecium, irrespective of their destination, whether staminal or staminodal.

From this stage onwards, in those primordia that belong to the innermost whorl and in a varying number of primordia that belong to the next outer whorl, the subsequent development of the sporogenous tissue be-

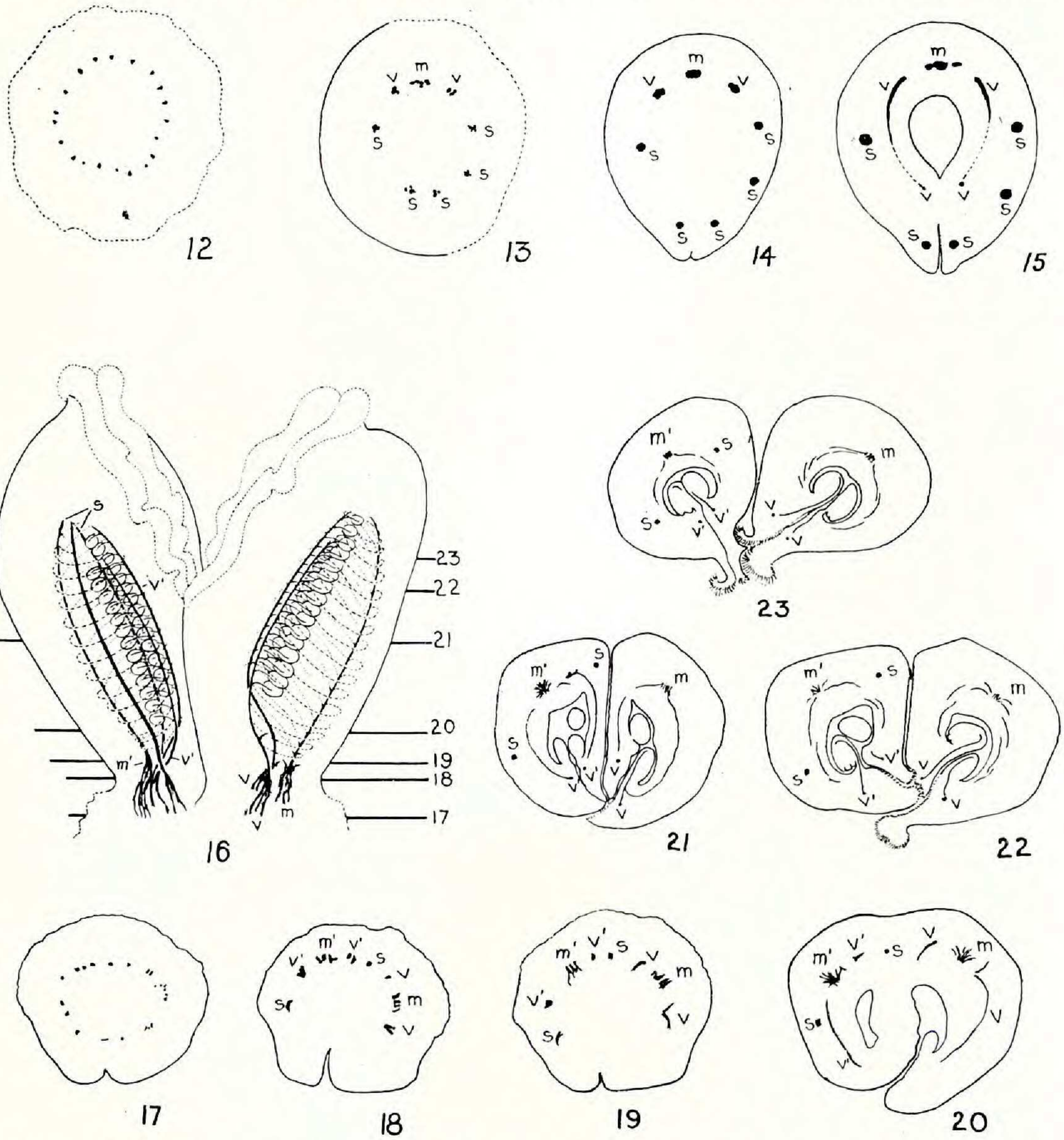
comes arrested and all the cells excepting the procambial strand become rapidly parenchymatized. By further differentiation of the component cells and by a modification of the external form, the appendages become staminodes. On the other hand, the development of the sporogenous tissue continues in the remaining primordia and the rate of parenchymatization of the cells becomes somewhat retarded, so that an abaxial patch of darkly staining cell layers still persists (compare the staminodes and the stamens in *Fig.* 85). These appendages mature into stamens.

Thus it will be seen that both the staminodes and stamens show a fundamentally similar origin and development until a certain stage, and the factors that make them develop into one or the other of these structures operate later; both structures are similar in their method of vascularization, although the marginal traces in the staminode divide once again. Furthermore, the stamens may often bear degenerate sporangia (1). All of these facts indicate that in *Degeneria,* the staminodes are best interpreted as sterile microsporophylls.

GYNOECIUM. — The gynoecium of *Degeneria* is represented by a solitary carpel occupying a terminal position on the floral axis. After supplying the members of the preceding whorls, a fairly large number of cauline bundles (varying usually between 18 and 25) are left over in the floral axis, *Fig.* 12. A few of these bundles, however, disappear at the base of the carpel; others recombine into seven to nine larger bundles, *Figs.* 13, 14. The three adjacently placed bundles (marked *m* and *v* in the figures) situated below the midrib region of the folded megasporophyll run into it as median and ventral traces; the other bundles (marked *s*) also enter the carpel and occupy positions in its wall as indicated in the illustrations, *Fig.* 15. The median trace gives out extensive side branches, which spread in the carpellary walls in a pinnate manner, *Figs.* 24–27. The ends of the branches finally anastomose with the ventral trace of the corresponding side. The branches of the ventral traces and to a small extent those of the dorsal trace take part in the vascularization of the ovules, as will be explained in a later paragraph. In contrast to the behavior of the ventral and median traces, the extra traces (marked *s*) in the carpel remain distinct and isolated — in location as well as in the degree of branching — from the system of the median and ventral traces. Even in the mature fruit, they persist as robust cords, maintaining the same configuration, *Fig.* 29. In other words, in spite of the fact that several traces enter the carpel, only three of them (the median and ventrals) behave as normal carpellary traces, whereas the others do not; the presence and behavior of the median and ventral traces in the carpel is typical and consistent, whereas the number of the extra traces is subject to fluctuation. This situation leads one to suspect strongly that the extra traces do not belong to the integral vascular system of the carpel and to conclude that the carpel of *Degeneria* is essentially a three-trace megasporophyll as in the Winteraceae(2).

How then can the extra traces of the carpel be explained? What may be their possible significance? In this connection it is worth while to

recall the general behavior of floral apices in relation to vasculature. Unfortunately such studies have not been extended to a wide range of flowers. However, the information provided by Arber and other work-



FIGS. 12–23. *Figs. 12–15.* Transverse sections at successive levels starting from the base of the carpel. Explanation in text. *Fig. 16.* Semidiagrammatized pattern of vascularization in a two-carpelled gynoecium as seen from a side; reconstructed after a study of serial transverse sections. *Figs. 17–23.* Transverse sections of the two-carpelled gynoecium at levels indicated in Fig. 16 by corresponding numbers. All figs., × 10.

ers [3] is indicative of the following salient generalizations: In multi-carpellate flowers the vascular bundles of the axis that are left over after supplying the perianth and androecium take part in the vascularization of the carpels in a normal and uniform manner. Thus all vascular bundles are "used up" by the carpels. This seems to be the usual behavior in the great majority of instances. But, particularly in genera

[3] See Arber, A. "The interpretation of the flower: A study of some aspects of morphological thought," Biol. Rev. 12: 157–184. 1937, and literature cited therein.

and species that exhibit a series in the reduction of many carpels to one, the following modifications are frequently seen, either singly or in various combinations. (i) The vascular bundles (residual vascular tissue) that would have supplied the missing carpel or carpels may still persist in the floral axis either as such or after anastomosing with one another in various ways. (ii) The residual bundles may disappear at a considerable distance below the persisting carpel or carpels. (iii) They may fuse with the bundles that are concerned in supplying the persisting carpel or carpels. (iv) They may enter the persisting carpel itself as supernumerary traces.

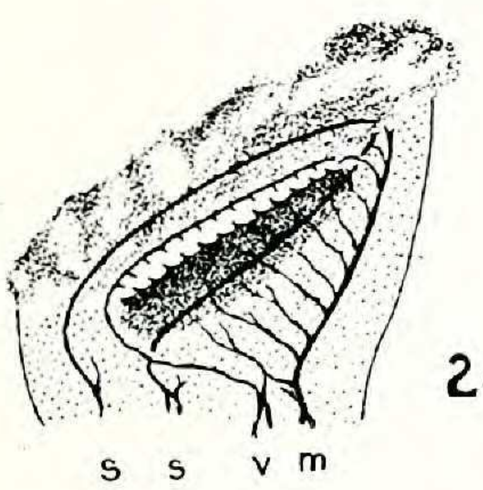
The situation in *Degeneria* seems to be a combination of the factors involved in items (i) and (iv). It may now be recalled that in *Degeneria* a large number of the stelar bundles are left over in the floral axis at the base of the carpel; that these fuse with one another into seven to nine larger bundles; that three of them form the median and ventral traces of the carpel; that the other extra bundles also enter the carpel and travel throughout its entire length; and that the behavior of the extra bundles within the carpel is markedly different from that of the median and ventral traces. The extra bundles therefore probably represent those that formerly supplied other carpels. In other words, the ancestral flower of *Degeneria* was in all probability multicarpellate. That this was most likely the actual condition is further supported by the method of vasculature of a bicarpellate flower.

Very rarely, flowers of *Degeneria* bear two carpels, attached at slightly different levels on the thalamus, *Figs.* 16–23. A transverse section just below the level of attachment of the carpels, *Fig.* 17, shows the bundles of the axis arranged in a ring in the same manner as in a monocarpellate flower, compare *Fig.* 12. The bundles unite in various ways with one another resulting in eight larger bundles, *Fig.* 18. The three bundles disposed towards the right hand side (marked *m, v*) supply the median and ventral traces to the first carpel. Of the remaining five bundles, the middle three (marked *m′, v′*) form the median and ventral traces of the second carpel; the other two bundles (marked *s*) also enter the upper carpel as supernumerary traces and behave in the same manner as in the case of the normal monocarpellate flower, that is, remain distinct from the integral vascular system of the carpel.

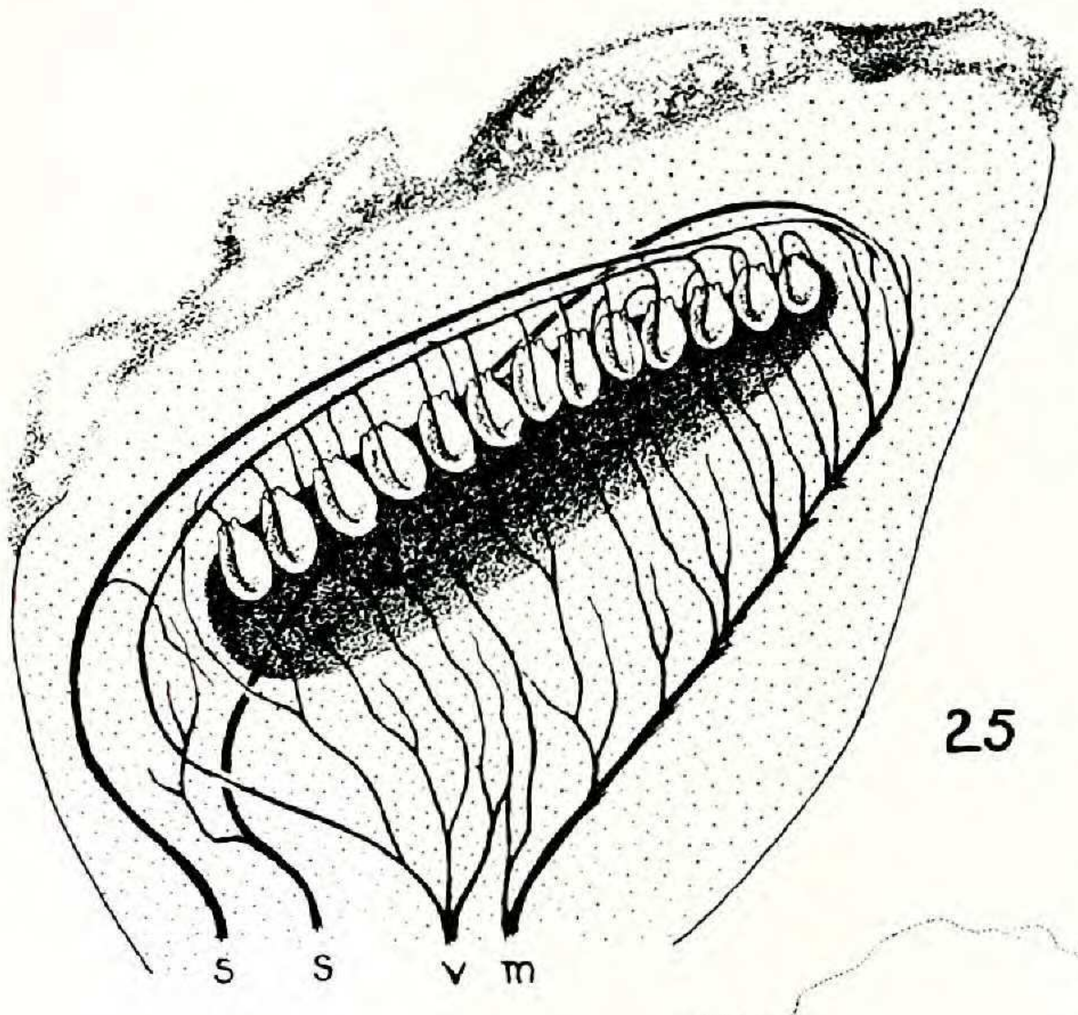
Two significant points emerge from this data. (i) The first carpel on the axis does not present any anomalies in its vascularization. (ii) The ultimate carpel receives only two extra traces in contrast to the monocarpellate gynoecium of the normal flower, where the number of such traces is larger, four to six. In other words, with more numerous carpels on the floral axis, the number of extra traces in the ultimate carpel becomes reduced and probably eliminated. Conversely, the presence of supernumerary traces in the normal monocarpellate flowers of *Degeneria* is closely associated with the phylogenetic reduction in the number of carpels.

VASCULARIZATION OF THE OVULES. — At the very base of the carpel, the ventral trace gives off two or three side branches which further ramify

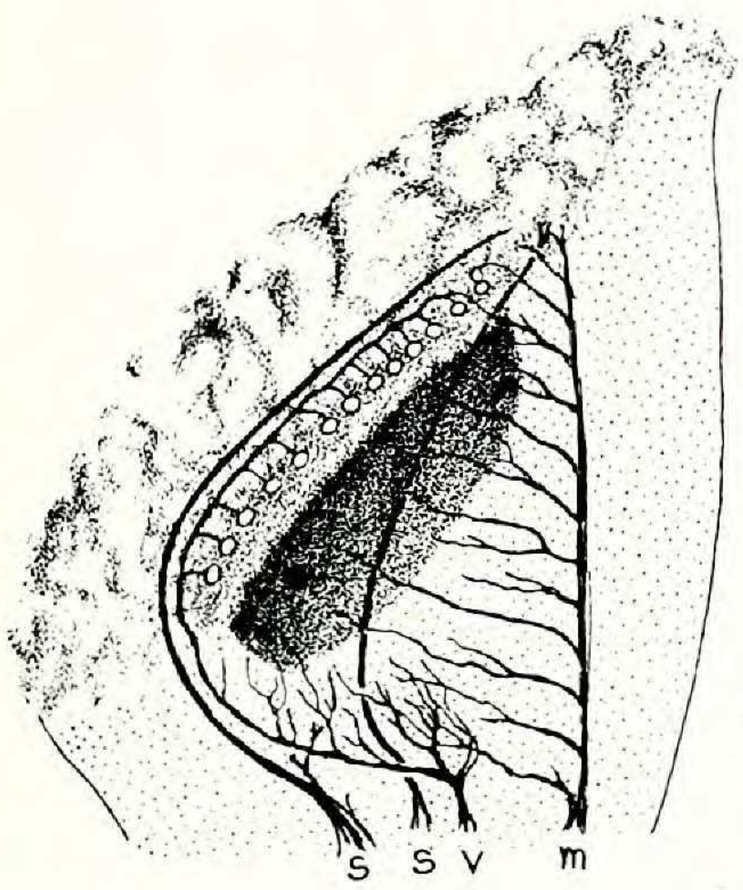
and anastomose with the system of the median trace, *Figs. 24–27.* The remainder of the trace continues to run along the ovule-bearing region. In general, this trace remains relatively weakly developed and on this account there is every possibility of overlooking its presence and at the



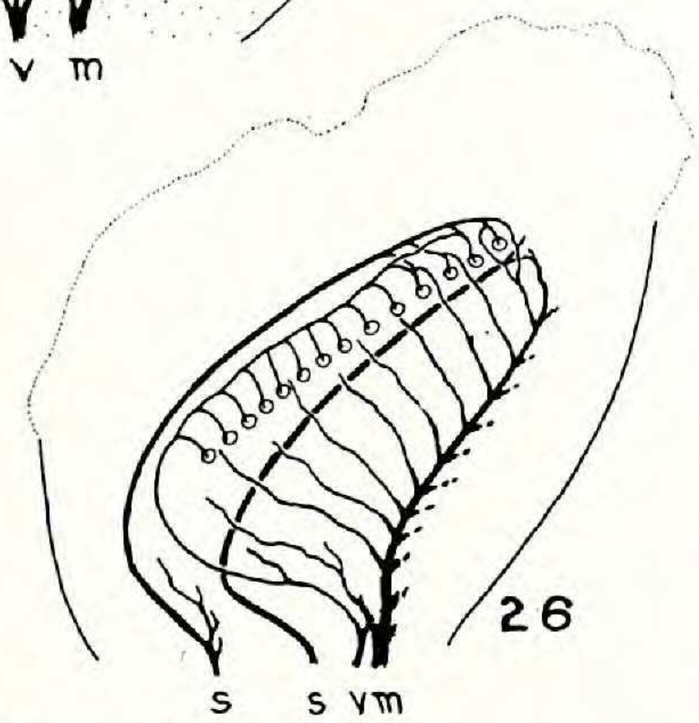
24



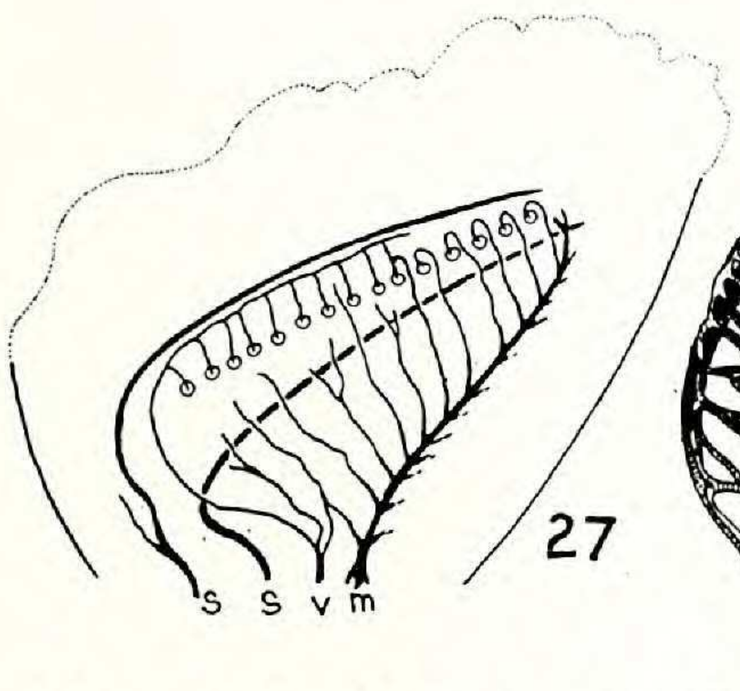
25



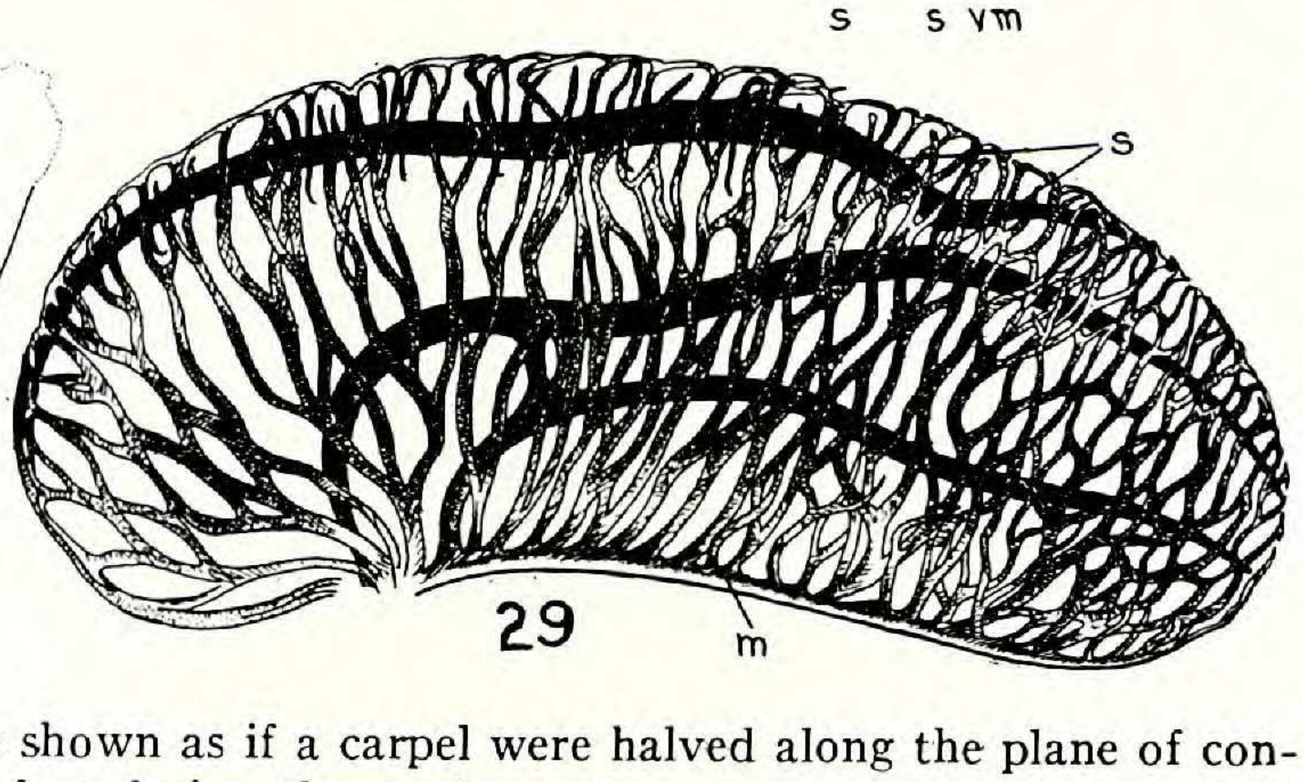
28



26



27



FIGS. 24–29. All figures are shown as if a carpel were halved along the plane of conduplication with the split surface facing the reader. *m* — median trace; *v* — ventral trace; *s* — supernumerary trace. *Fig. 24.* Vascularization of the carpel at the time of origin of ovular primordia, × 25. *Fig. 25.* Same, at anthesis, × 25. *Figs. 26* and *27.* Variations in the vascularization of the ovules at anthesis. Small circles denote the funicles with the ovules removed. Semidiagrammatic, × 17. *Fig. 28.* Drawing to show the expanse of the papillate stigmatic surface at anthesis; note its extension towards the interior of the carpel beyond the ovule-bearing region; ovules are removed and their respective places of attachment are denoted as empty circles, × 20. Also compare figs. 52 and 87. *Fig. 29.* Vasculature of mature fruit, × 2.5.

same time mistaking the otherwise well developed supernumerary trace, *s* in *Figs.* 24–27, 41–44, for the ventral.

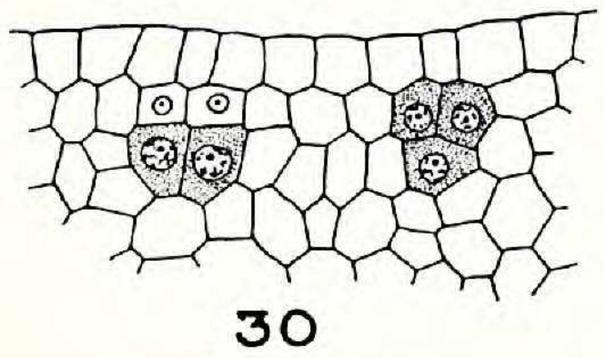
The ventral trace is concerned with the vascularization of the majority of the ovules. It sends out a number of slender branches all along its length and each branch enters an ovule. This pattern is stabilized in the ovules that are situated towards the basal region of the carpel. On the other hand, some of the ovules that are situated especially towards the distal end exhibit an altogether different situation. It has been pointed out that the median trace of the carpel builds up an extensive branch system and that the branches reach towards the ventral traces with which they ultimately fuse. Frequently, some of the branches of the median system fuse with the ovular traces given out by the ventrals (see the penultimate ovules towards the distal end in *Fig.* 25), whereby such ovules should be considered as having been vascularized by both the median and ventral systems. Less frequently the ventral trace is precociously used up and the distally situated ovules derive their vascular supply only from the median system, *Fig.* 27. In very rare instances, the supernumerary traces may also send out one or two slender branches that fuse with those of the distally situated ovular traces, *Fig.* 26. These various methods of vascularization often occur in the same carpel in varying combinations and fluctuate from carpel to carpel.

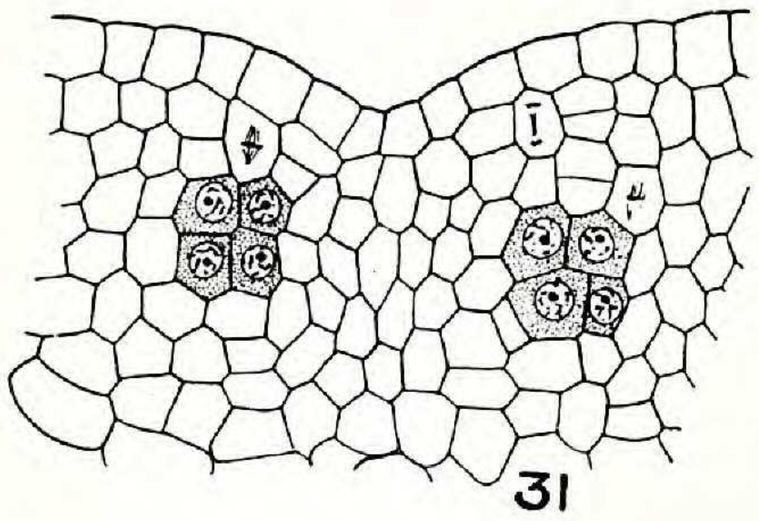
MICROSPORANGIUM AND MICROSPORES

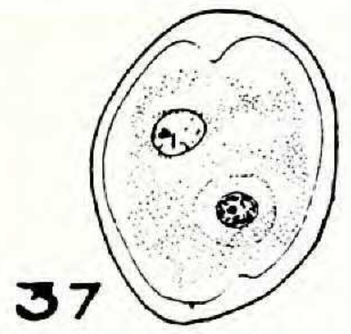
As pointed out by Bailey and Smith (1), the microsporangia are immersed beneath the abaxial surface of the sporophyll. As already mentioned on a previous page of the present contribution, the primary archesporium differentiates in the hypodermal layer of the abaxial surface. This fact negates any suggestions that the extrorse dehiscence in *Degeneria* is due to an ontogenetic shift in the position of the sporangia.

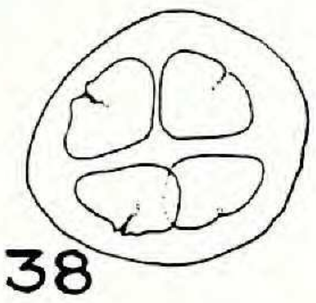
Although the primary archesporial cells are strictly hypodermal in origin, occasionally one or two cells belonging to the sub-hypodermal layer also show the characteristics of archesporial cells (group of three cells in the right side of *Fig.* 30). It is quite possible that the cells of the sub-hypodermal layer may infrequently become a part of the archesporium and share its subsequent development. Two adjacent groups of archesporial cells, each group consisting of two or three cells as seen in transverse sections, are differentiated between the median and marginal traces of the sporophyll. The first division in the archesporium results in the formation of parietal and sporogenous layers, *Fig.* 30. The parietal layer by further periclinal divisions builds up four or five wall layers and the tapetum, whereby the sporogenous cells become deep-seated in the tissue of the sporophyll, *Fig.* 31. The outermost of the wall layers later transforms into the endothecium. The sporogenous cells also may divide once and thus increase in number before differentiating as microspore mother cells.

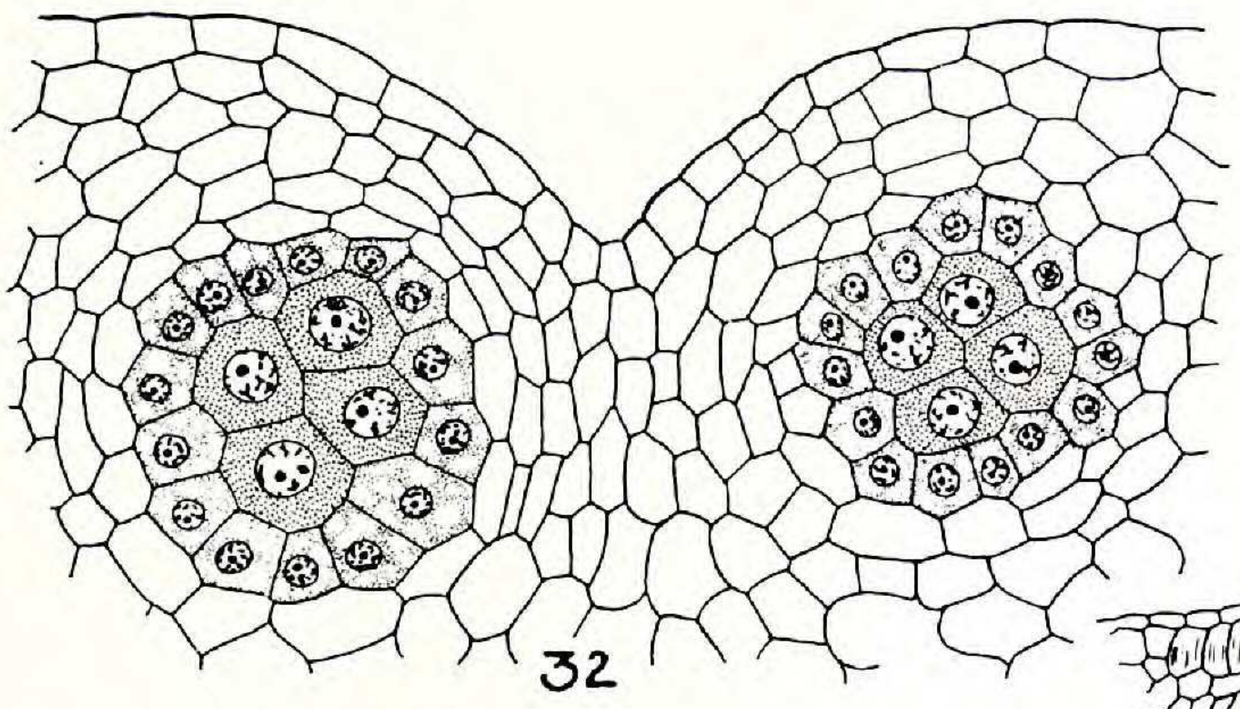
Simultaneously with their enlargement, the microspore mother cells become jacketed by a continuous layer of tapetum, *Fig.* 32. When the

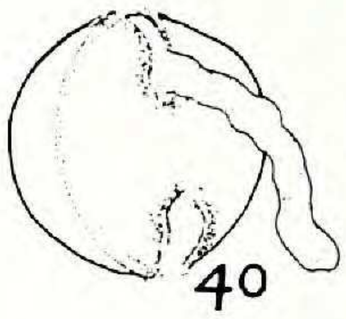


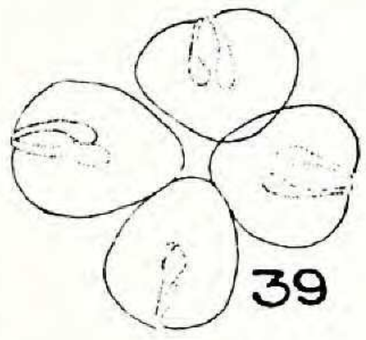


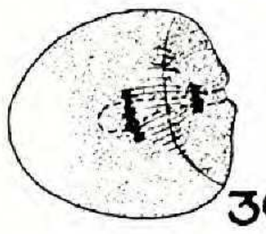


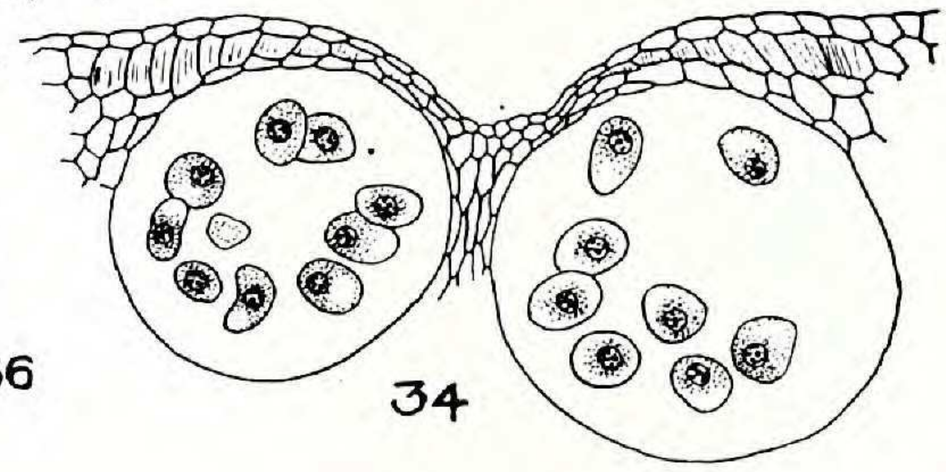


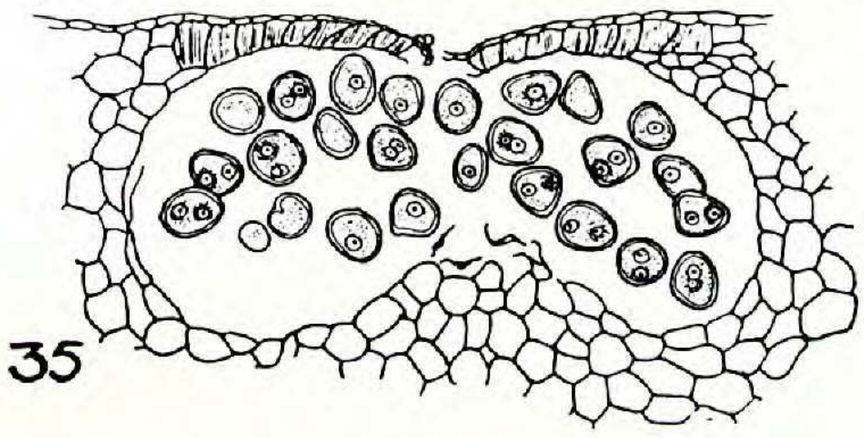












FIGS. 30–40. *Fig. 30.* Two adjacent groups of sporogenous cells of one half of the microsporophyll. In the right group, the archesporium is shown, in the left it has divided into the parietal and sporogenous layers, × 200. *Fig. 31.* Same, showing the differentiation of wall layers; the primary sporogenous cells have also divided, × 200. *Fig. 32.* Same, showing the organization of tapetum, × 200. *Fig. 33.* A single sporogenous group with its tapetum, some of the tapetal cells are binucleate and the nuclei in others are in various stages of division or reunion, × 200. *Fig. 34.* Two adjacent sporangia showing the disappearance of the tapetum, uninucleate microspores and the initiation of the endothecial thickening, × 50. *Fig. 35.* Same, at the shedding stage; the pollen grains are two-celled, × 50. *Fig. 36.* Division of the microspore. The broken line indicates the position of the germinal furrow, × 200. *Fig. 37.* Pollen grain at the shedding stage showing the faintly-stained vegetative nucleus and the darkly stained generative cell, × 200. *Fig. 38.* A young tetrad showing the initiation of the furrow on the distal face of each spore, × 135. *Fig. 39.* Pollen grains of a tetrad immediately after separation, showing the well defined furrow, × 135. *Fig. 40.* A germinated pollen grain removed from the papillate surface of a carpel; note the emergence of the tube from the broadened end of the furrow, × 200.

nucleus of the microspore mother cell is in the prophasic stages of the first meiosis, the tapetal cells become binucleate, *Fig.* 33. Frequently some of the nuclei fuse again and occasionally redivide. However, they do not migrate out of their cells and their general behavior is in conformity with the secretory type of tapetal organization. The cells of the tapetum function actively until after the first division of the microspore mother cell and then degenerate.

The microspore mother cell undergoes the meiotic divisions in a simultaneous manner and produces a tetrad of microspores. Usually, the configuration of the latter is tetragonal, *Figs.* 38, 39, rather than tetrahedral. The young microspore, while it is still lodged within the original wall of the mother cell, shows a conspicuous fold on its distal face, *Fig.* 38. At the time of separation of microspores from the tetrad, *Fig.* 39, a narrow groove with slightly broadened extremities takes the place of the distal fold. It is this groove that differentiates as the germinal furrow (colpa) of the mature pollen grain. Thus it is clear that the position of the germinal furrow in the pollen of *Degeneria* is distal.

The uninucleate microspores, *Fig.* 34, soon become scattered in the sporangial cavity. The nucleus of the microspore migrates towards the distal side of the spore and a vacuole develops towards the proximal side. The first division of the spore nucleus is accomplished in this position. The orientation of the spindle during this division is such that the generative cell is always cut off towards the furrow-end of the grain, *Fig.* 36, that is, towards the exterior end of the tetrad. The generative cell, after a time, shifts its position and comes to lie nearer the interior of the grain, *Fig.* 37. The pollen grains are shed in this two-celled condition.

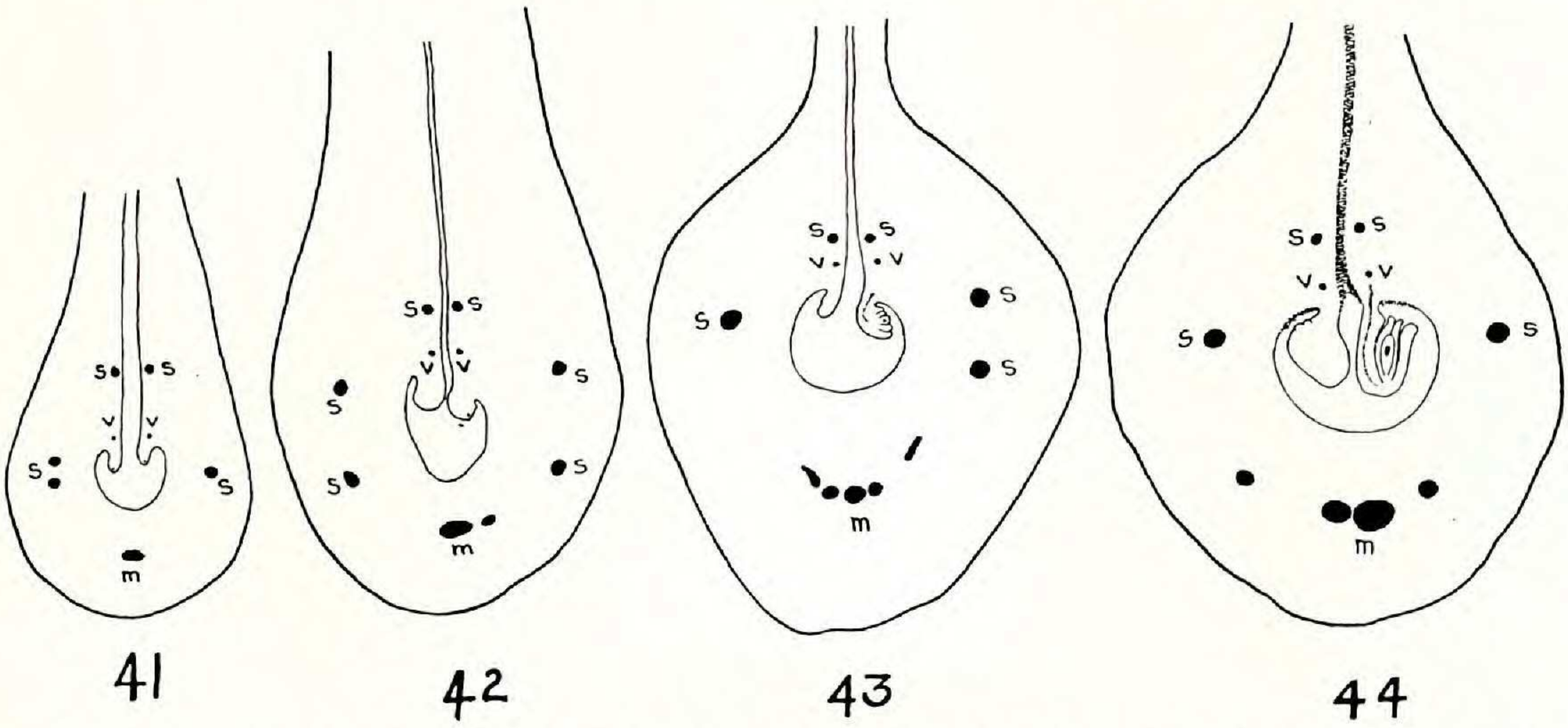
At the time of the division of the microspore nucleus, the cell layers separating the adjacent sporangia break down and their cavities become continuous. The endothecium is characteristically localized in disposition, not extending beyond the outer faces of the sporangia, *Fig.* 35.

MEGASPORANGIUM AND FEMALE GAMETOPHYTE

The ovule-bearing region of the carpel is situated far back of the margins of the conduplicately folded carpel, a feature clearly demonstrated in transverse sections, *Figs.* 41–44, 88–91. Longitudinal sections passing through the plane of conduplication also reveal the same feature, *Fig.* 86, and in addition, reveal the slanting orientation of the carpellary cavity and the ovule-bearing region in conformity with the abaxial deformation of the carpel. A single row of ovular primordia arises opposite each of the ventral bundles, *Figs.* 41, 88. Ten to thirteen primordia constitute a row and the ovule-bearing region itself is confined to the upper end of the carpellary cavity.

The ovular primordia grow into the cavity at first in a vertically downward direction, *Figs.* 41, 88. With the differentiation of the nucellus and integuments, the apex of the ovule undergoes a curvature of 90°, *Figs.* 42, 43, and by the time of sporogenesis, becomes bent on itself, thereby assuming a completely anatropous position, *Figs.* 44, 91.

Soon after the differentiation of the archesporial cell in the nucellus, the two integuments originate more or less simultaneously, *Fig.* 47. When the megaspore mother cell is fully differentiated, the inner integument comes to have three layers of cells and the outer, four to five layers. The number of cell layers in the integuments continue to increase and at the time of fertilization the inner integument consists of four cell layers at the region of the micropyle, but remains three layered in the part sur-



FIGS. 41–44. Transverse sections of carpels at different stages of development to show the curvature undergone by ovular primordia in assuming the anatropous position, × 12. *m* — median trace; *v* — ventral trace; *s* — supernumerary trace.

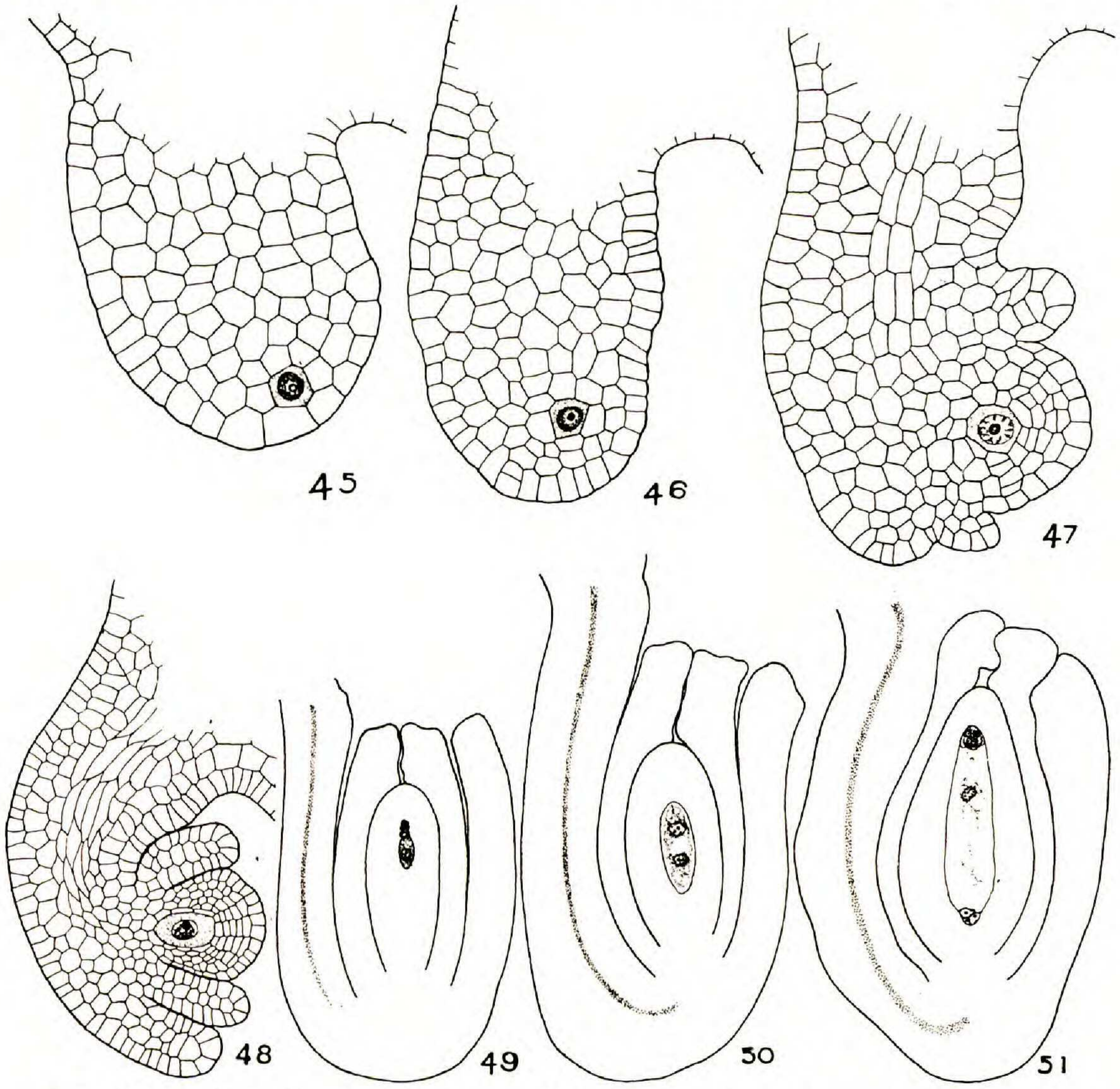
rounding the nucellus; the outer integument comes to have seven or eight layers. As will be shown later, the thickness of the outer integument becomes further increased during post-fertilization development. Both integuments of the mature ovule envelop the nucellus completely and the inner integument organizes the micropyle, *Figs.* 49–51.

The subepidermal archesporial cell, *Fig.* 45, divides into a parietal and a sporogenous cell. The former gives rise to seven to ten layers of parietal tissue that cap the gametophyte; some of the layers persist in the developing seed for a long time, *Fig.* 101. The sporogenous cell functions as the megaspore mother cell, *Figs.* 46–48 and after undergoing the reduction divisions gives rise to a linear tetrad of megaspores, the chalazal one of which develops into the eight-nucleate gametophyte, *Figs.* 49–51. The fusion of the polar nuclei takes place usually before fertilization. However, in a few cases it may be postponed until the intervention of the sperm. The antipodals organize into cells and show signs of degeneration before the ovules are fertilized.

STIGMA, POLLEN TUBE, FERTILIZATION

It should be emphasized again that the ovule-bearing region of a *Degeneria* carpel does *not* represent the margin of the carpel and that the ends of the flared-out region of the sporophyll are the true margins. During earlier stages of development, *Fig.* 88, the closely approximated ventral surfaces of the conduplicate carpel form an open cleft extending

from the locule to the exterior. Later, when the ovular primordia are differentiating into nucellus and integuments, the ventral halves of the conduplicate carpel tend to flare apart externally, *Fig*. 89. The epidermal cells of the adaxial surfaces in the region of this flaring develop into pro-

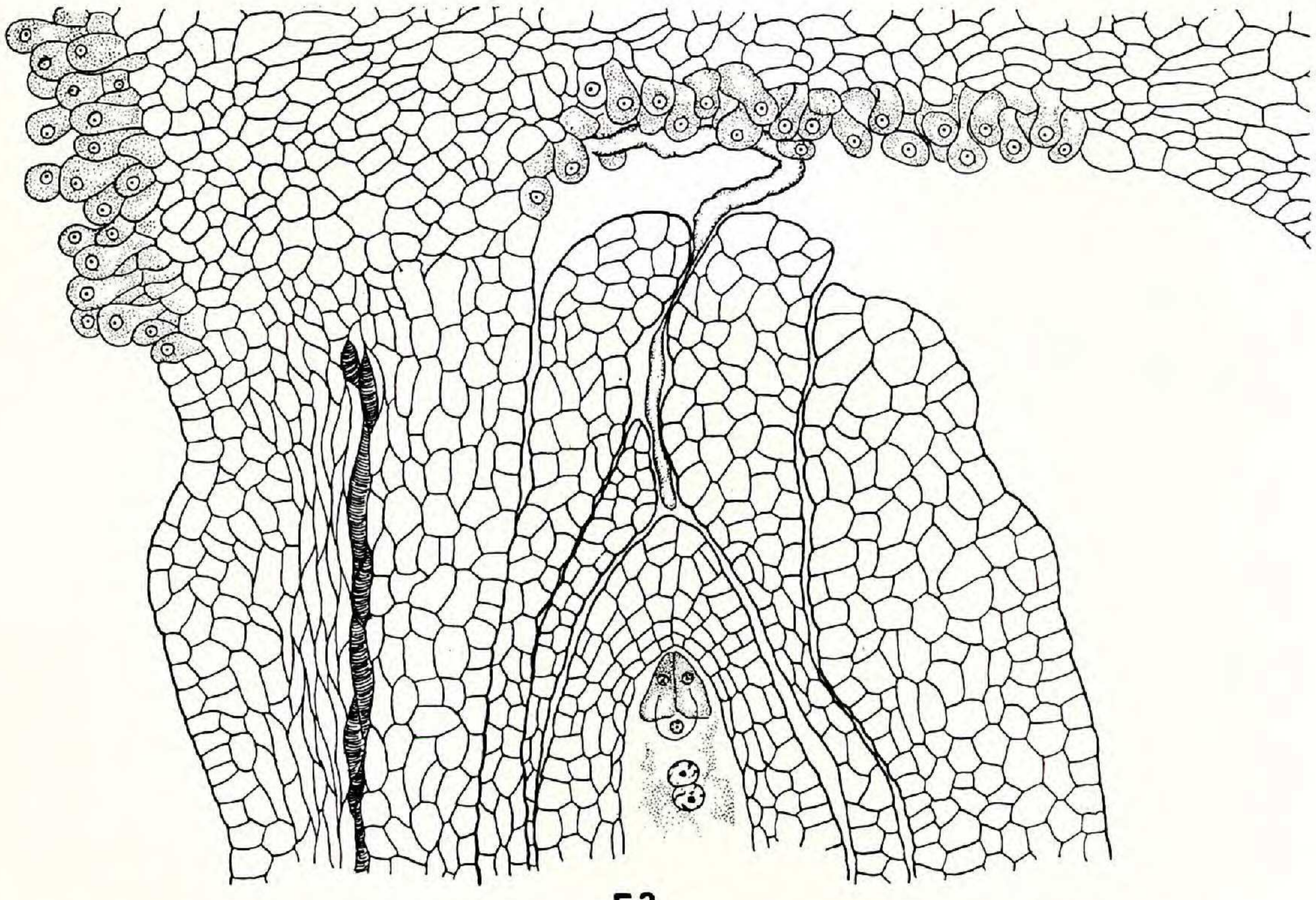


FIGS. 45–51. Figs. 45, 47 and 48 are enlarged from Figs. 41–43 respectively and are mounted with their corresponding orientation. *Fig. 45.* Archesporial cell in the nucellus. *Fig. 46.* Formation of parietal cells. *Fig. 47.* Origin of the integuments. *Fig. 48.* Megaspore mother cell in synizesis; parietal cells have increased in number. *Fig. 49.* Linear tetrad of megaspores, the chalazal one enlarging. *Fig. 50.* Two-nucleate embryo sac. *Fig. 51.* Mature eight-nucleate embryo sac. Figs. 45–48, × 182; Figs. 49–51, × 40.

tuberant hairs, *Figs*. 89, 93. This wave of glandular differentiation spreads outward toward the margins of the carpel and inward into the locule, *Fig*. 90, ultimately extending internally beyond the region of attachment of the ovules, *Fig*. 87. As a result, the narrow cleft between the adaxial surfaces that lie outside the ovule-bearing region becomes occluded by a closely interlocking system of papillate hairs, *Figs*. 90, 91, 94. At anthesis, the hairs on the flaring region grow into a dense felt and many of the individual hairs become two- or three-celled, *Fig*. 95, whereas

in the locule they do not become as long or multicellular. Thus, a greater portion of the adaxial surface of the sporophyll — from the margin to a considerable distance towards the interior of the ovule-bearing region — becomes evenly papillate, *Fig*. 28. As will be shown presently, this entire surface is concerned in the penetration of the pollen tube and hence "stigmatic."

An examination of alcohol-preserved specimens reveals that during pollination the pollen grains become deposited anywhere on the adaxial surfaces of the outwardly flaring parts of the carpel. A few grains were also found attached on the abaxial surface; however, none of these grains show any signs of germination and appear to have lost their cell contents through degeneration. This observation indirectly emphasizes the importance of the papillate surface as an essential factor in the germination



52

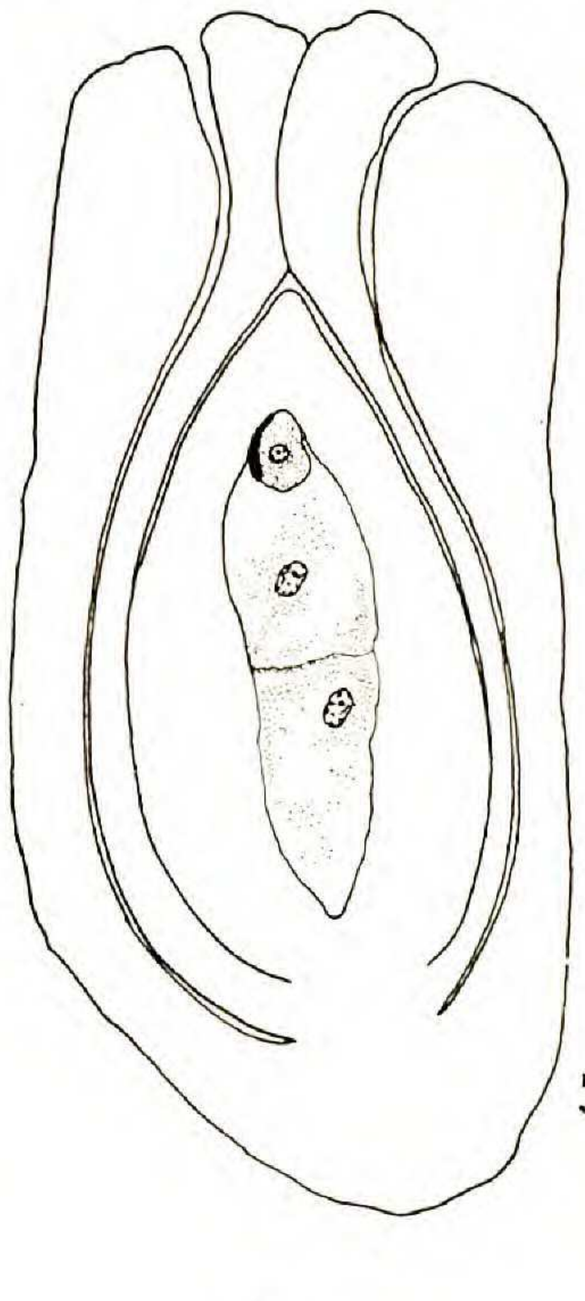
FIG. 52. Micropylar half of a mature ovule with a part of its funicle and associated carpellary tissue showing the papillate epidermis, the course of the pollen tube, etc., × 210.

of the pollen grains in *Degeneria*. The grains that are lodged on the hairy surface put forth pollen tubes. The tube arises not from the narrow region of the germinal furrow but rather from one of its broadened ends, *Fig*. 40. The course of the tube into the carpellary cavity is strictly along the papillate surface and at no time does the tube penetrate the carpellary tissue. Upon reaching the ovule-bearing region, it continues to grow between the funicles and reaches the extension of the papillate surface on the inside of the ovule-bearing region. Here the tube wanders about a little and then characteristically curves back and enters the micropyle, *Fig*. 52.

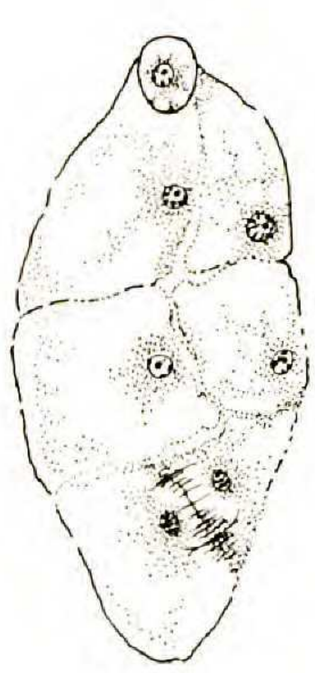
After reaching the lower end of the micropylar canal, the tube bores through the apex of the nucellus until the upper end of the embryo sac is reached. During the discharge of the pollen tube contents into the embryo sac, one of the synergids is usually destroyed. Double fertilization takes place in a typical manner. Triple fusion precedes syngamy.

ENDOSPERM, EMBRYO

The first division of the primary endosperm nucleus results in a transverse chambering of the embryo sac, *Fig.* 53. The separating membrane is very thin and delicate. The nuclei of both chambers divide almost simultaneously and in quick succession, each division being followed by wall deposition until the embryo sac cavity becomes filled with a mass of extremely thin-walled cells, *Figs.* 54–58. The sequence of the divisions, however, does not follow any prescribed method. The tissue keeps on steadily increasing at the expense of the nucellus and finally occupies

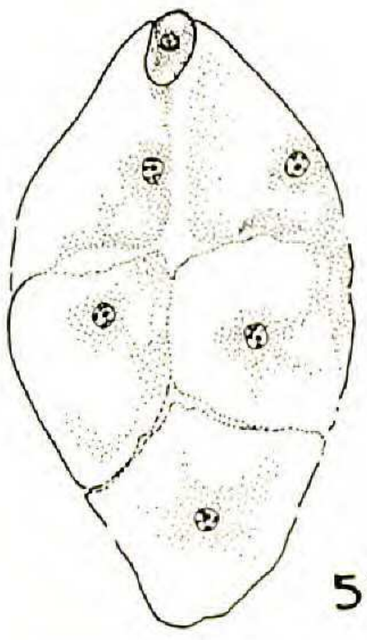


53

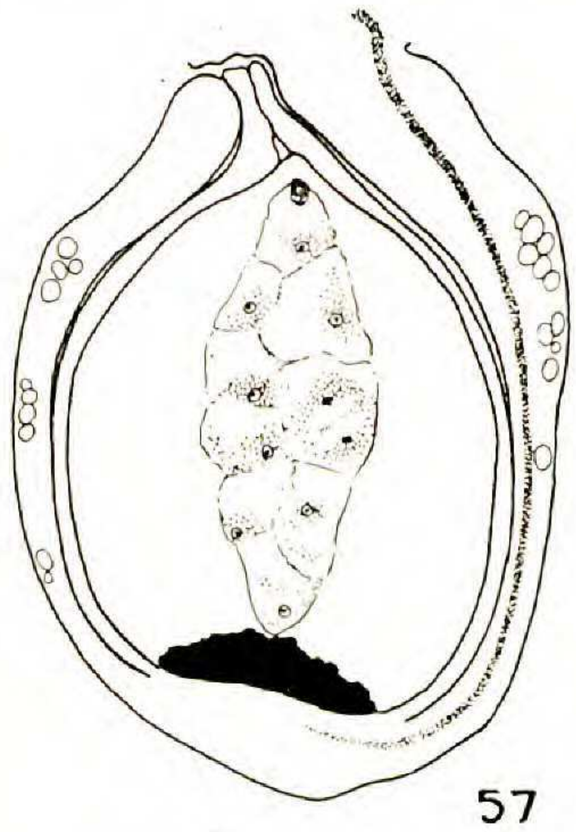


54

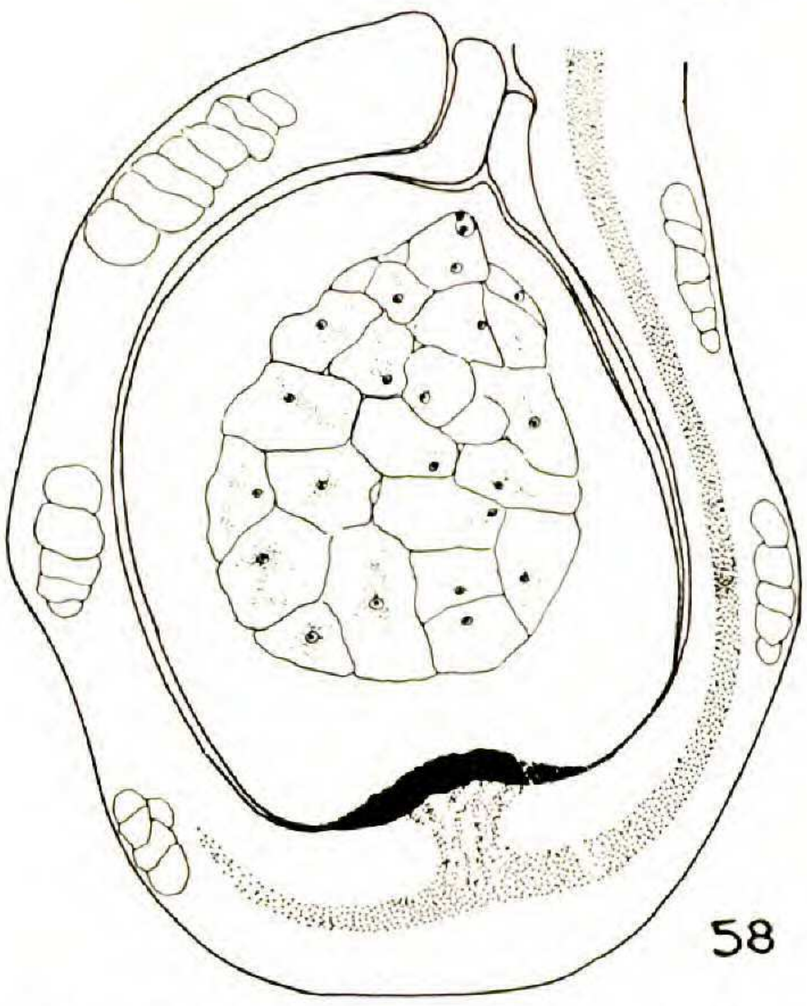
56



55



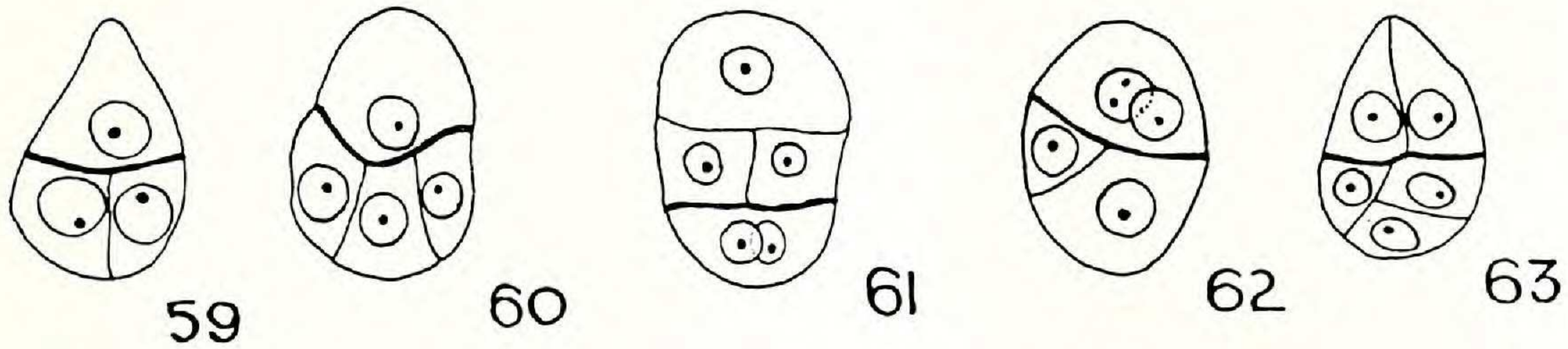
57

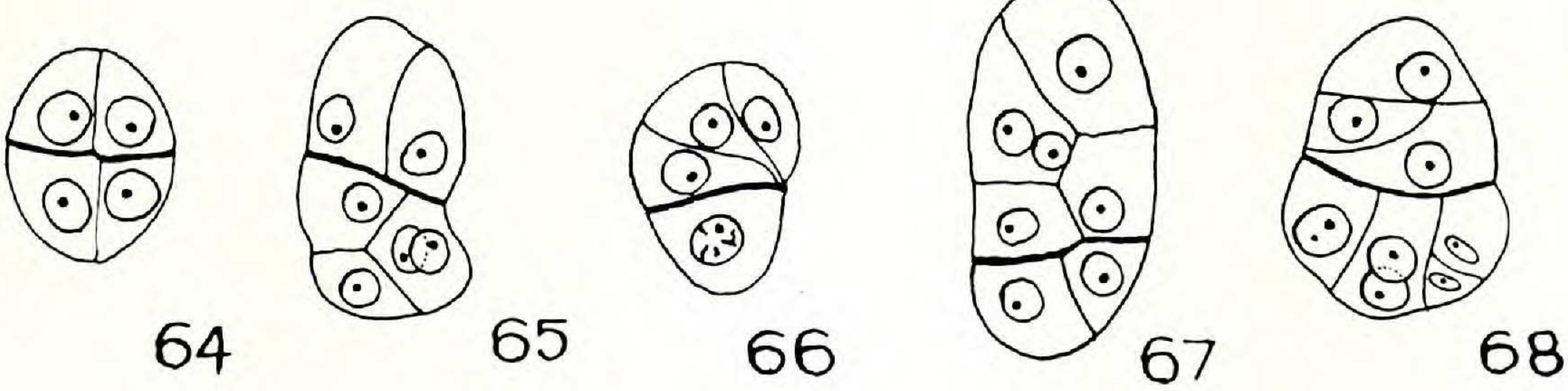


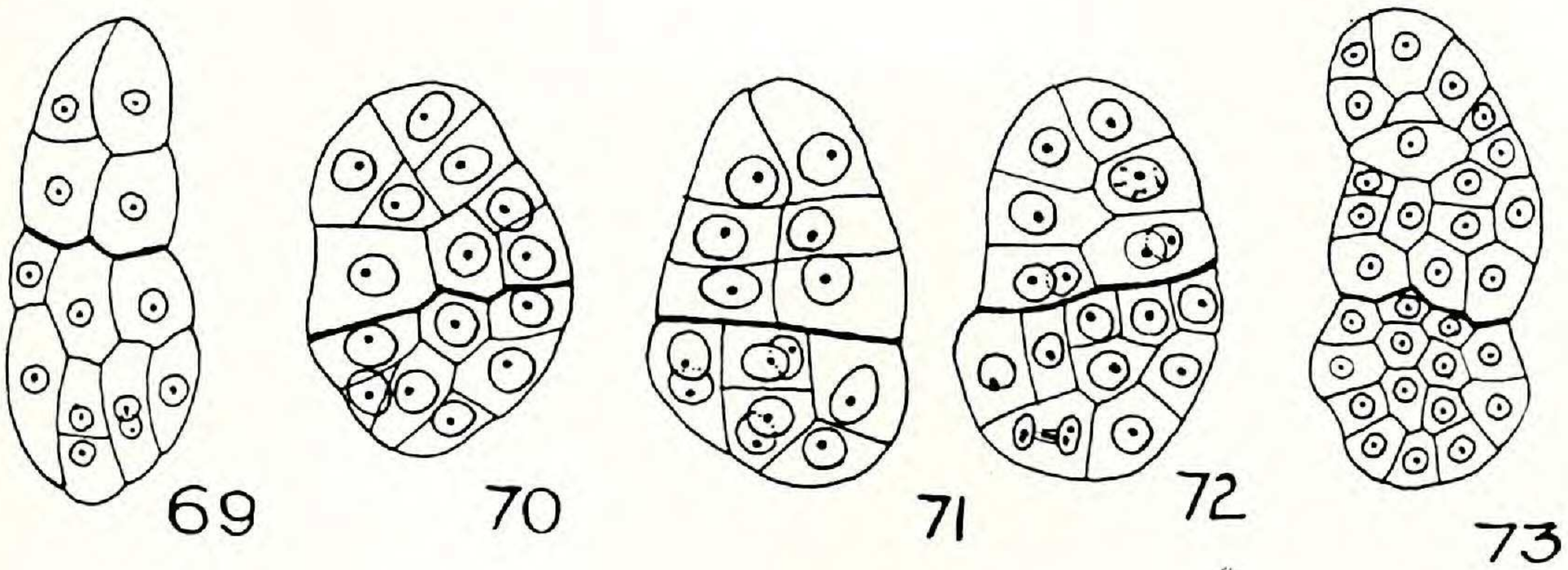
58

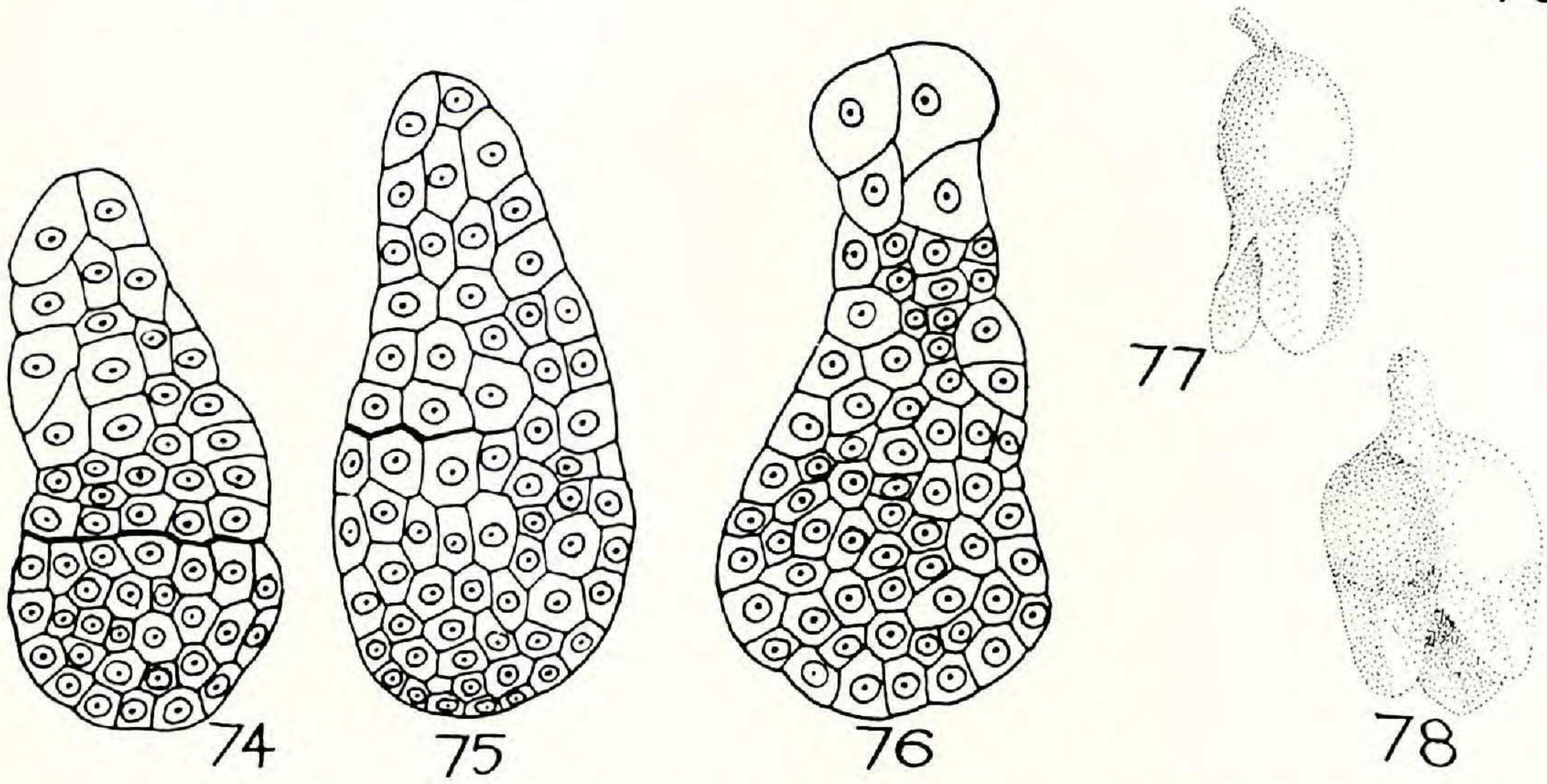
FIGS. 53–58. *Fig. 53.* An ovule showing two-celled endosperm and zygote, × 40. *Figs. 54–56.* Early stages in the development of endosperm, × 100. *Figs. 57, 58.* Slightly later stages; note the differentiation of oil-bearing cells in the outer integument, the pad of degenerated nucellar cells (shown in black) at the chalaza and the extension of the vascular bundle on to the opposite side in Fig. 58, × 30.

the entire space enclosed within the integuments. The development of ruminations in this tissue will be considered in connection with the seed.









FIGS. 59–76. Stages in the development of embryo; explanation in text. The heavy transverse line in the figures denotes the boundary of the cells derived from the basal and terminal cells of the two-celled proembryo, × 283. FIGS. 77, 78. Embryos dissected from mature seeds; note the three cotyledons, swollen hypocotyl and stalk-like suspensor, × 90.

The zygote divides only after about 300 endosperm cells are formed. The first division is in a transverse plane and results in the formation of basal and terminal cells. The subsequent method of segmentation does not follow a strict pattern, as may be seen from *Figs.* 59–69. However, when a fairly large amount of material is studied, certain broad trends of developmental pattern suggest themselves. The second cell generation commences first in the terminal cell and this is invariably by a vertical wall, whereas the segmentation of the basal cell is generally delayed, *Figs.* 59, 60, 65. The division in the latter cell also is usually by a vertical wall, *Figs.* 62–65, thus resulting in two superposed tiers of two cells, *Fig.* 64; less frequently, the wall laid down is oblique or transverse. The division of the basal and terminal cells may be more or less simultaneous or in rare instances the development of the terminal cell lags behind, *Figs.* 66, 67. However, subsequent divisions follow in rapid succession, resulting in an ovoid mass of cells. The derivatives of the basal and terminal cells are distinguishable for a fairly long time, *Figs.* 73–75.

In spite of the highly plastic nature of the early segmentation, the method of tissue differentiation in the undifferentiated mass of cells is quite stabilized. All the derivatives of the terminal cell and about half of the derivatives of the basal cell enter into the construction of the embryo proper. The other half takes part in the construction of a massive suspensor. With the differentiation of the suspensor, the identity of the derivatives of the basal and terminal cells becomes obliterated, *Fig.* 76. In the mature embryo, the suspensor persists as a short stalk, *Figs.* 77, 78, 106; the hypocotyl region is bulbous; the cotyledons are well differentiated and three or rarely four in number. Internally, the stem and root apices, an incipient root cap and the procambial system are well organized. However, the size of the embryo is significantly small in relation to the large amount of endosperm, *Fig.* 79.

The cotyledonary number in *Degeneria* is remarkable. In *Magnolia grandiflora* (4) and possibly in other species of this family, tricotyledonous embryos are encountered occasionally as abnormalities. On the other hand, a tricotyledonous development in *Degeneria* seems to be the rule, as not even a single instance of an embryo with two cotyledons was seen among the large number of seeds examined. The following data give an

COLLECTION NUMBER	NUMBER OF SEEDS EXAMINED	TRICOTYLEDONOUS EMBRYOS	TETRACOTYLEDONOUS EMBRYOS
5880	a. 42 from 3 fruits	34	8
	b. 50 free seeds	44	6
6190	a. 46 from 4 fruits	39	7
	b. 50 free seeds	40	10
6318	a. 72 from 6 fruits	63	9
	b. 50 free seeds	42	8
	310	262 or, nearly 87%	48 or, nearly 13%

estimate of the frequency of the occurrence of the tricotyledonous and tetracotyledonous embryos in *Degeneria*.

The embryogeny of magnoliaceous species such as *Magnolia virginiana* (5), *M. grandiflora* (4), *M. Soulangeana, Michelia fuscata, M. Champaca* and *Liriodendron tulipifera* (unpublished observations of the author) presents several points of similarity with *Degeneria*. The plasticity in the developmental pattern of the two-celled proembryo, the organization of an oval mass of undifferentiated cells before tissue differentiation, the development of a massive suspensor and its persistence in the mature embryo, the swollen nature of the hypocotyl, the nearly triangular shape of the cotyledon, and finally the size relationships of the mature embryo and endosperm, are the more significant resemblances. Although the embryos of *Degeneria* are prevailingly tricotyledonous, such tricotyledonous nodes are of not infrequent occurrence in large populations of seedlings of magnoliaceous plants.

SEED

Fertilization affects not only the structures within the embryo sac but also other parts of the ovule. The fertilized ovule undergoes enormous increase in size and the unfertilized ones soon degenerate, *Fig*. 97. In the former, the nucellar cells abutting upon the antipodal end of the embryo sac soon begin to degenerate and stain very deeply, *Fig*. 96. With subsequent growth of the ovule, the mass of degenerating cells becomes compressed in the form of a pad, *Figs*. 57, 98. More and more nucellar cells in the chalazal region become involved and cause an expansion in the width of the pad, *Fig*. 58. During later stages, this structure becomes very prominent and is contacted by the ramifications of the vascular bundle of the ovule, *Figs*. 99, 100. Some of the magnoliaceous genera also exhibit a similar feature in varying degrees.

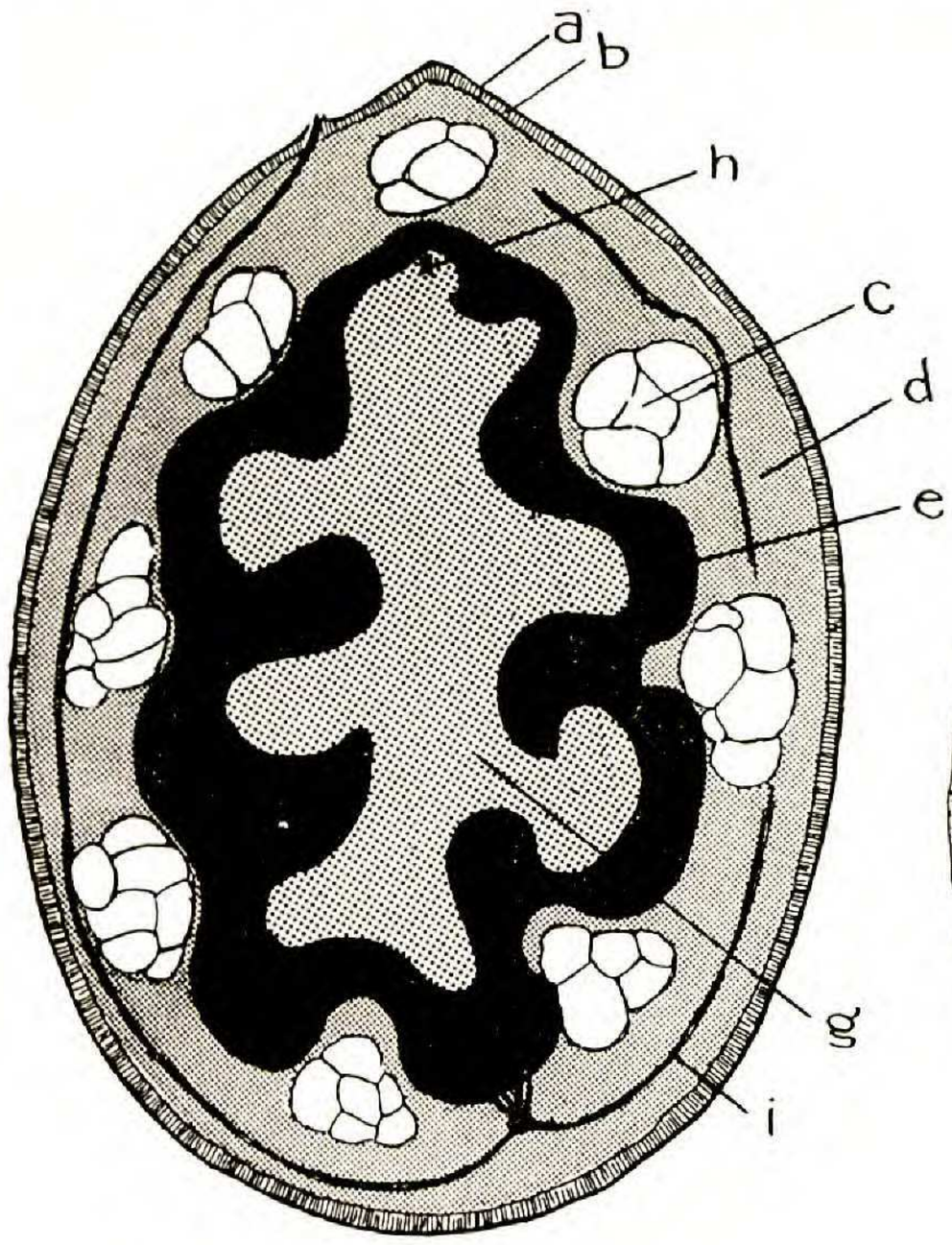
At the time of fertilization, the outer integument consists of about eight layers of cells, all the cells appearing homogeneous. After fertilization, clusters of two to ten cells in the outer layers develop into oil-bearing cells, *Figs*. 57, 58, 99. Some of the walls of the oil cells break down during later stages to result in cyst-like cavities. In the mature seed they become very conspicuous and occupy a more superficial position, *Figs*. 79, 100, 102.

Hand in hand with the early segmentation of the zygote, localized patches of cells from the innermost layers of the outer integument begin rapid divisions largely by tangential walls and grow out in the form of wedges, *Fig*. 102. Thus the entire inner surface of the outer integument is thrown into ridges of varying pitch and the continuously increasing endosperm occupies the contour of this surface. The exterior of the mature endosperm thus becomes irregularly grooved and cleft, *Figs*. 79, 105, and presents all the essential characteristics of a ruminated type.

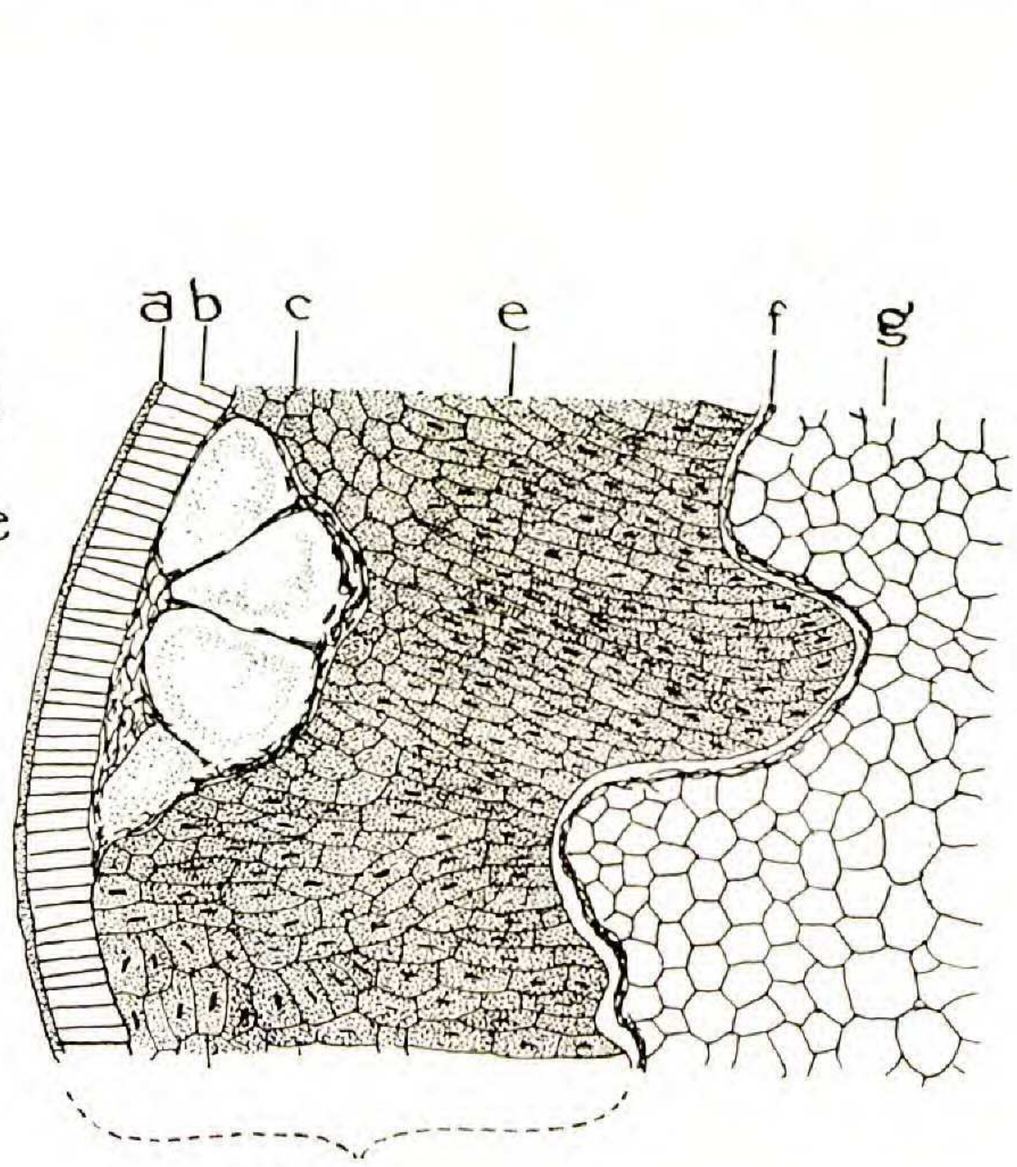
It must be emphasized that the nature of the rumination in *Degeneria* is less exaggerated than in Annonaceae, Myristicaceae, Palmae, etc. In these families, the ingrowths of the integument penetrate the endosperm

far deeper in the form of thin transverse plates, whereas in *Degeneria,* they are more massive and wedge-shaped than plate-like; also, in the families cited above, the partitions are more or less transverse and parallel to one another, or extend in a converging manner from the periphery, thus exhibiting a specialized manifestation, whereas in *Degeneria* the wedges are scattered indiscriminately and the form of the individual wedges is somewhat fluctuating. In some members of the Myristicaceae (6), it is the inner integument that takes part in the organization of the rumination, but in *Degeneria* it is clearly the outer.

The epidermis of the mature seed becomes covered by a thick cuticle and the epidermal cells undergo conspicuous elongation in a radial direction, *Figs.* 79, 80. That part of the outer integument wherein the oil cells are located continues to persist as a succulent outer coat. The inner



79



80

FIGS. 79, 80. *Fig. 79.* Diagrammatic representation of a median longitudinal section of a mature seed, the plane of section passing through the vascular bundle, × 20. *Fig. 80.* A portion of the seed coat and endosperm of Fig. 79 enlarged to show the histological details, × 40. *a* — cuticle; *b* — epidermis; *c* — oil-bearing cells; *d* — fleshy coat; *e* — stony coat; *f* — inner integument; *g* — endosperm; *h* — embryo; *i* — vascular bundle.

part together with its ruminated outgrowths undergoes considerable hardening and transforms into an inner stony coat, *Figs.* 79, 80, 102. The process of hardening first commences in the cells of the wedges and gradually works outward. Due to the uneven pattern of hardening, the stony coat becomes irregularly ruminate on its outer surface also, *Figs.* 79, 103.

The inner integument becomes crushed into a membranous covering between the endosperm and the stony coat. The vascular bundle extends to the opposite side of the funicle as far as the micropylar end, *Fig*. 79.

At this point, a reference to the nature of the hardening material in the cells of the stony coat deserves special mention. In *Degeneria,* as also in magnoliaceous genera, the cells become filled with vacuolar substances during development and finally the entire cell contents are rendered excessively hard; the cell walls, however, remain thin and the cells do not increase in size, *Fig*. 80. Thus the hardness in these cases is due to the transformation of the cell contents. On the other hand, in the corresponding tissue of annonaceous genera, the cell walls become heavily lignified and the individual cells elongate in the form of sclerotic fibres; the secondary thickening frequently occludes the cell lumen. Thus the hardening is due to the lignification of the cell walls. This important feature serves to distinguish the seeds of the Magnoliaceae and Degeneriaceae from those of the Annonaceae.

The mature seeds of the families Degeneriaceae, Magnoliaceae and Himantandraceae share several features in common, at the same time showing significant differences in histological details. In all the three families, the inner integument is reduced to a membranous layer and the outer integument increases in thickness during post-fertilization development and takes part in the construction of the seed coat; the vascular bundle becomes extended from the chalazal side toward the micropyle; and the minute embryo is embedded in an extensive endosperm. The seeds of the Degeneriaceae and Magnoliaceae are highly opaque, oval or round with a fleshy exterior, whereas those of the Himantandraceae are decidedly less opaque, suborbicular, greatly compressed and submembranous. The outer integument differentiates into fleshy and stony coats in the former families, whereas in the latter, such a differentiation is wanting; instead, the outer cell layers attain a cartilaginous texture. The fleshy layer in the Degeneriaceae and Magnoliaceae contains the oil-bearing cells. In the former family, their distribution is characteristically in clusters and in the latter, isolated and diffuse. Whether the seed coat of *Himantandra* contains oil cells could not be determined from herbarium specimens. The nature of hardening of the stony coat is essentially similar both in the Degeneriaceae and Magnoliaceae. The epidermal cells lining the exterior of the seed in the Magnoliaceae and Himantandraceae are isodiametric in shape, whereas in *Degeneria* they are conspicuously elongated radially.

FRUIT

Long before anthesis, the carpellary wall differentiates into two regions. The cells of the outer region stand out more prominently with their darkly staining walls and protoplasts in contrast to the faintly staining inner region, *Fig*. 81. After fertilization, important changes occur within each of them. The cells of the outer region appear to be retarded in

meristematic activity, numerous spicular cells develop, and the vascular system built by the median trace becomes excessively ramified. On the other hand, the cells of the inner region suddenly step up their meristematic activity and grow into the carpellary cavity in the form of lobes of a spongy consistency. The lobes intrude between the developing ovules, at the same time overtaking the degenerate ones and pushing them to one side, *Fig.* 97. Ultimately the entire capillary cavity is densely packed with the spongy ingrowths, *Figs.* 98, 99, and the interior of the fruit becomes fleshy. The outer region of the carpellary wall, in which the spicular cells and vascular system ramify, becomes increasingly tough and coriaceous.

According to field observations of Dr. Smith, the fruits dehisce along the ventral suture after falling from the tree. The seeds become disseminated through this split, also perhaps facilitated by the decay of the coriaceous wall. In such fruits, the vascular skeleton built by the median and ventral traces appears as a coarse and closely woven mesh, and the supernumerary vascular traces, which have now assumed the form of large cords, clasp the outer surface of the mesh, *Fig.* 29.

The observation of Bailey and Smith (1) that the seeds of one row are strictly sessile, while those of the other row are borne on slender elongated funicles, needs to be amended in view of the large amount of material now available. Although such a condition occurs in a few instances, it is subject to numerous exceptions. Sessile as well as long-funicled seeds are indiscriminately distributed and invariably the former outnumber the latter. Furthermore, the distinction between the two categories is one of degree. The manifestation of these conditions seems to be largely dependent upon the degree and direction of pressure exerted by the invading spongy lobes of the carpellary wall on the developing seeds. The rate of ingrowth is by no means uniform and simultaneous throughout the surface, especially in the early stages. If the activity of the spongy ingrowth in the immediate vicinity of the micropylar end of the seed dominates, it is likely that the ovule in question is carried more towards the interior of the carpel, whereby the funicle also becomes correspondingly stretched. On the other hand, if the activity of the lobes from the opposite direction dominates and tells upon the chalazal region of the ovule, it is possible that the funicle is not subjected to extensive stretching. It may be further noted that such a differential method of growth of the carpellary wall is also responsible for the frequent readjustment or reorientation of the seeds in the mature fruit.

In dried fruits, the fleshy region shrinks and is pressed back against the outer coriaceous wall. The latter becomes very hard, as might be anticipated in view of its high ratio of spicular cells and vascular elements. When the seeds are broken from their points of attachment with the carpellary wall, some of the shrunken spongy tissue also becomes detached and forms a cupule-like appendage on the micropylar end of the seed, as pointed out by Bailey and Smith (1). However, it must be borne in mind that the seed in reality has no true appendages and that what

appears to be a cupular appendage is clearly the dried remnants of the spongy ingrowth of the carpellary wall.

RELATIONSHIPS OF THE DEGENERIACEAE

A critical evaluation of the various vegetative and reproductive characteristics of *Degeneria, Himantandra* and the Magnoliaceae (sensu strictu) with regard to their mutual affinities and systematic position has already been published by Bailey and his coworkers (1, 3). Only a few points that are not covered by them will be dealt with here.

The vascularization pattern of the cotyledonary node of *Degeneria* differs from that in most of the investigated species of Magnoliaceae. In *Degeneria,* each of the three or four cotyledons has a trilacunar attachment, whereas in most Magnoliaceae the four lateral strands of the paired cotyledons arise by the bifurcation of two traces, each related to an independent gap. When three cotyledons are formed, the six lateral strands arise by the bifurcation of three independent traces. However, a nodal anatomy resembling that of *Degeneria* has been reported in *Magnolia Soulangeana* (7) and may ultimately be found to occur in seedlings of other representatives of the Magnoliaceae.

The nodal anatomy and the vascularization of the adult petiole follow a characteristic and basically similar plan in the Degeneriaceae, Magnoliaceae and Himantandraceae, a fact that has already been recorded (3). Furthermore, in the case of the Degeneriaceae and Magnoliaceae, there are similar transitions between the trilacunar nodes of the first seedling leaves and the multilacunar nodes of leaves from older plants. The emarginate nature of the first one or two leaves succeeding the cotyledons characterizes *Degeneria* and is of not uncommon occurrence in Magnoliaceae.

During microsporogenesis, the method of differentiation of the parietal and sporogenous tissues, the organization of a binucleate secretory tapetum from the innermost layer of the parietal cells,[4] the simultaneous method of meiosis, the prevalence of a tetragonal arrangement of the microspores at the tetrad stage, the cutting off of the generative cell towards the exterior side of the tetrad, and the two-celled shedding condition of the pollen grains are features shared by both *Degeneria* and the Magnoliaceae. The broad microsporophylls of *Degeneria* and *Himantandra,* bearing long, slender, deeply embedded sporangia have similar counterparts in certain representatives of the Magnoliaceae. However, the stamens of this family differ from those of *Degeneria* and *Himantandra* in having a less typically parenchymatous hypodermal layer.

The origin and differentiation of the nucellus, the thin inner and thick outer integuments, the formation of seven to ten parietal layers in the ovule, the monosporic eight-nucleate embryo sac and the ephemeral nature

[4] Maneval (5) reports that the tapetum in *Magnolia virginiana* is cut off from the sporogenous cells. This observation seems to be erroneous. In *M. Soulangeana, M. stellata,* as well as in *Michelia fuscata* and *Liriodendron tulipifera,* I have seen only a parietal origin of this layer.

of the antipodals of *Degeneria* are present point by point in the Magnoliaceae. The *ab initio* cellular endosperm,[5] the excessive broadening of the chalazal region of the ovule, and the development of the darkly-staining pad of degenerated nucellar cells at the chalaza are again a combination of characters that are common to *Degeneria* and the Magnoliaceae; the presence of the last two characters in *Himantandra* appears to be almost certain, as can be judged from herbarium material. In *Degeneria* the endosperm becomes ruminated, and this feature has no counterpart either in the Magnoliaceae or in *Himantandra*.

The plasticity in the sequence of early cell divisions in the two-celled proembryo, the organization of a massive suspensor which is not clearly delineated from the body of the embryonal mass in the early stages, and the bulbous nature of the hypocotyl in the mature embryo are a set of characters in the magnoliaceous embryogeny. The overwhelming proportion of tricotyledonous embryos appears to be confined to *Degeneria* alone.

The outer integument takes part in the construction of the seed coat and the vascular bundle extends on the opposite side in the seed in all the three families, and the inner integument is reduced to a membranous layer. In *Degeneria* and the Magnoliaceae, the outer integument differentiates into fleshy outer and stony inner coats; such a distinction is absent in *Himantandra,* and instead, some of the outer cell layers become modified so as to render the seed coat cartilaginous. The stony coat of *Degeneria* is ruminate internally as well as externally, whereas that of the Magnoliaceae is smooth; however, the histological nature of hardening in both families is identical. Although the fleshy coat of *Degeneria* and the magnoliaceous genera contains oil cells, the pattern of distribution is different in the two families.

The fruit of *Degeneria* is relatively large as compared with that of *Himantandra* or of the Magnoliaceae. Its interior is packed with fleshy outgrowths of the carpellary tissue and the seeds become embedded in it. In the Magnoliaceae, the fruit is either dry or succulent and in *Himantandra,* fleshy. However, in the fleshy fruits of the latter families, the carpellary wall does not form spongy lobes that embed the seeds as in *Degeneria.*

It will be evident from the brief review presented above that a large number of embryological characters are common to all three families. Nevertheless, the dissimilar characters are seen in specific combinations in each of them. Thus the summation of evidence again points to the

[5] Earle (4) states that in *Magnolia grandiflora,* "The early divisions of the endosperm nucleus are very rapid and the number of free nuclei formed is comparatively small. . . . Wall formation occurs shortly after the appearance of these free nuclei . . .". But in *M. virginiana* (5), *M. Soulangeana, M. stellata, Michelia fuscata* and *Liriodendron tulipifera* (unpublished observations of the author), the endosperm is cellular from inception. The walls of this tissue in the early stages are extremely delicate and hard to see as also in *Degeneria,* unless the sections are counterstained with eosin or fast green. It is very likely that the presence of walls in *Magnolia grandiflora* escaped Earle's notice.

same conclusion already reached by Bailey, Nast and Smith (3) that "in the Degeneriaceae, Himantandraceae and Magnoliaceae we are concerned with three distinct but closely related families."

SUMMARY

Additional information on the anatomy of the secondary xylem, node, petiole, seedling, flower, fruit and seed of *Degeneria vitiensis* is presented.

Ontogenetic and anatomical evidence indicate that the staminodes are sterile microsporophylls in which the development of the sporogenous tissue becomes arrested.

After supplying the vascular traces to the perianth and androecial whorls, a large number of bundles are left over in the floral axis. They reunite into seven to nine larger bundles and enter the carpel. Only three of these behave as true carpellary traces. The remaining traces represent the residual vascular traces that once supplied the now missing carpels. The anatomy of bicarpellate flowers also supports the hypothesis that the ancestral flower of *Degeneria* was multicarpellate.

The ovules derive their vascular supply in part from the branches of the ventral veins, in part from those of the median vein, and in part from the branches of both sets of veins. The stigmatic papillae extend to a considerable distance towards the interior of the ovule-bearing region. The ontogenetic occlusion of the cleft of the carpel is accomplished by the interlocking arrangement of the papillae. The germination of the pollen grain and the path of the pollen tube is largely determined by this papillate surface.

The germinal furrow of the pollen grain develops on its distal face. A summation of evidence from the development of the gametophytes, endosperm and embryo, and the structure of the node, petiole, seed and fruit, confirms the earlier conclusion that in the Degeneriaceae, Himantandraceae and Magnoliaceae we are concerned with three distinct but closely related families.

LITERATURE CITED

1. Bailey, I. W. & A. C. Smith. Degeneriaceae, a new family of flowering plants from Fiji. Jour. Arnold Arb. 23: 356–365. 1942.
2. Bailey, I. W. & C. G. Nast. The comparative morphology of the Winteraceae. IJ. Carpels. Jour. Arnold Arb. 24: 472–481. 1943.
3. Bailey, I. W., C. G. Nast & A. C. Smith. The family Himantandraceae. Jour. Arnold Arb. 24: 190–206. 1943.
4. Earle, T. T. Embryology of certain Ranales. Bot. Gaz. 100: 257–275. 1938.
5. Maneval, W. E. The development of *Magnolia* and *Liriodendron,* including a discussion of the primitiveness of the Magnoliaceae. Bot. Gaz. 57: 1–31. 1914.
6. Mauritzon, J. Contributions to the embryology of the orders Rosales and Myrtales. Lunds Univ. Arsskr. N.F. Avd. 2, 35(2): 1–120. 1939.
7. Thomas, E. N. Seedling anatomy of Ranales, Rhoeadales and Rosales. Ann. Bot. 28: 695–733. 1914.

EXPLANATION OF PLATES

PLATE I. FIGS. 81–87. *Fig. 81.* Transverse section of a flower bud long before anthesis; perianth removed, × 16. *Figs. 82–85.* Longitudinal sections of flower buds at different stages of development, × 10. *Fig. 86.* Longitudinal section of a young carpel in the plane of conduplication to show the alignment of ovules and the slanting position of the carpellary cavity, × 21. *Fig. 87.* Transverse section of a portion of a carpel at the time of fertilization to show the extension of the papillate epidermis on the inner side of the ovule-bearing region (indicated by arrow), × 50. *m* — micropylar canal occluded by papillae.

PLATE II. FIGS. 88–95. *Figs. 88–91.* Transverse sections of carpels at different stages of development of the papillate epidermis. *Fig. 88.* Very young stage; the adaxial surfaces do not show any papillate differentiation at this stage (detail in Fig. 92). *Fig. 89.* The epidermal cells of the flaring ventral surfaces are beginning to protrude (detail in Fig. 93). *Fig. 90.* The epidermal papillae have developed toward the interior of the carpel and the cleft has become plugged (detail in Fig. 94). *Fig. 91.* At anthesis. The papillae of the flaring ventral surfaces have elongated and a large number of them have become two- or three-celled (detail in Fig. 95). Figs. 88–91, × 21; Figs. 92–95, × 64.

PLATE III. FIGS. 96–102. *Fig. 96.* An ovule after fertilization. Note the degenerated and darkly-staining nucellar cells at the chalazal end of the ovule, × 38. *Fig. 97.* Transverse section of a young fruit to show the ingrowth of the carpellary wall in the form of spongy lobes. Also note the development of spicular cells in the outer layers of the carpel, × 23. *Fig. 98.* A portion of the transverse section of a fruit, slightly older than in Fig. 97. The spongy tissue is invading between the ovules. The darkly-staining chalazal pad is increasing in breadth (compare the seed in Fig. 58, which is from a corresponding stage in development), × 20. *Fig. 99.* Same, at a still later stage. The ovule is cut somewhat obliquely. The characteristic distribution of oil cells, the chalazal pad and its connection with the vascular bundle, and the effect of the ruminate outgrowth of the inner surface of the outer integument on the endosperm, are clearly seen, × 18. *Fig. 100.* Detail of the chalazal region of a young seed at a stage similar to Fig. 99, showing the pad and its relation to the surrounding tissue, × 20. *Fig. 101.* Micropylar region of a young seed (outer integument removed) showing the endosperm and embryo. Note the persistence of parietal cells in contact with the suspensor-end of the embryo, × 40. *Fig. 102.* A portion of a young seed in section showing the wedge-shaped ruminate outgrowths from the inner surface of the outer integument, × 30.

PLATE IV. FIGS. 103–106. *Fig. 103.* External surface of the mature stony coat of the seed, × 10. *Fig. 104.* Internal surface of the same, × 10. *Fig. 105.* Endosperm dissected from an immature seed to show the early stages of rumination, × 10. *Fig. 106.* A group of mature embryos, × 30.

INSTITUTE FOR RESEARCH IN GENERAL PLANT MORPHOLOGY,
HARVARD UNIVERSITY.